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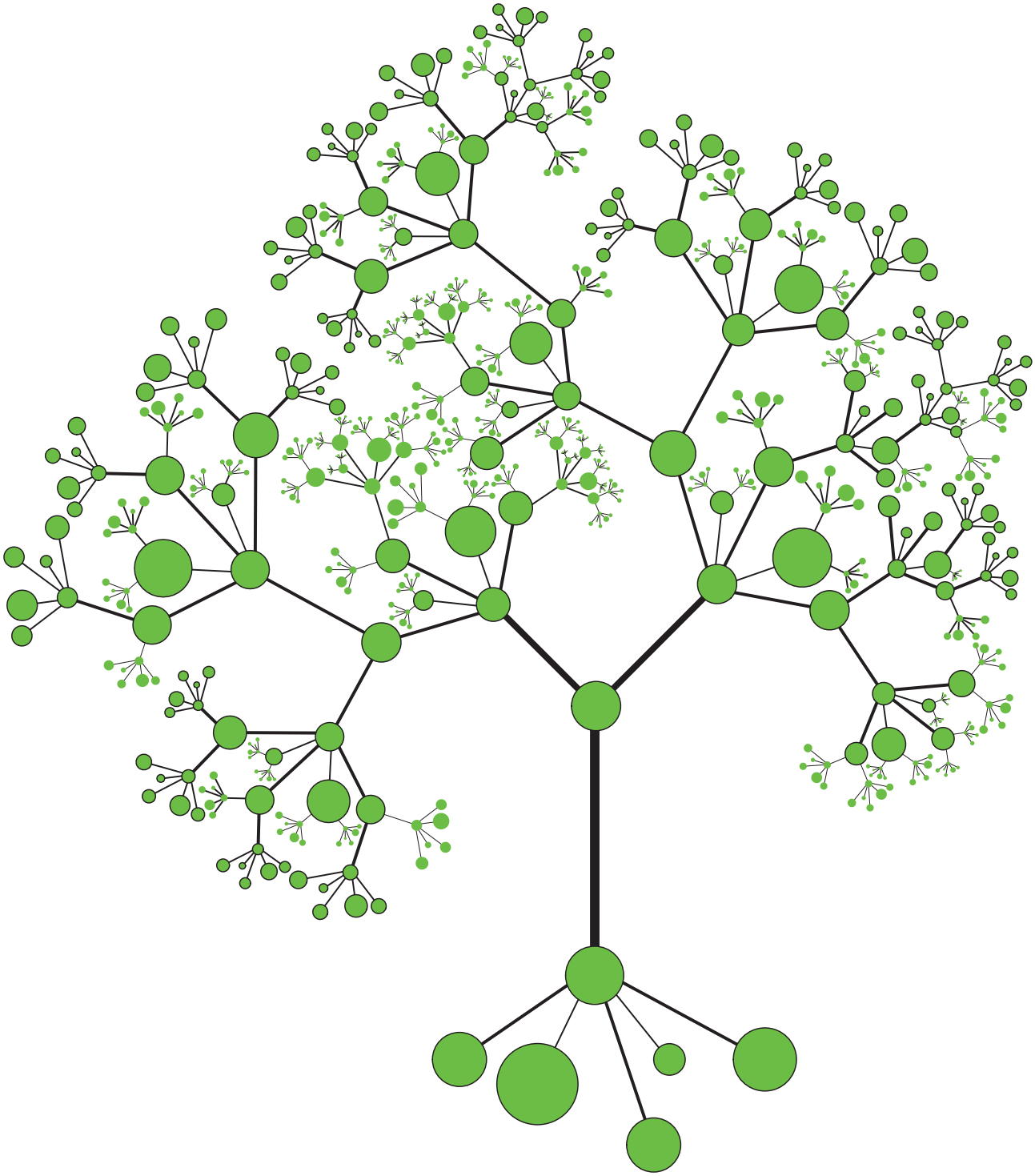
Spatial dynamics, robustness and scaling up to pollinators



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Dissertation for Doctor of Philosophy in Ecology.
Accepted by the Faculty of Science at the University of Zurich.
Financially supported by the
Swiss National Science foundation (PZ00P3_148261).

Edited in LaTeX.

Cover picture *Mutating fractal*

Plant Interaction Networks

Spatial Dynamics, Robustness and Scaling Up to Pollinators

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

von

Gianalberto Losapio

aus

Italien

Promotionskommission

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Zürich, 2017

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Summary

In alpine ecosystems, harsh environmental conditions make plants' lives difficult: drought, low temperature, poor soil and strong winds are some of the problems plants have to cope with to survive and reproduce. Three decades ago, ecologists started to report that plants can cooperate with neighbouring species to survive in such stressful ecosystems. Since then, hundreds of studies have been conducted looking at positive interactions — facilitation — in plant communities. Nevertheless, few works have investigated the network of interactions among plant species and the consequences of these interactions for other trophic levels in the ecosystems. Consequently, it is unclear how plant interaction networks are assembled across space, how they respond to environmental change and how they are linked to mutualistic networks.

The overall aim of this work is to study plant interaction networks, looking at the plant community from a network perspective. The objective is to elucidate the nature of interactions among plants, the networks they build up within plant communities and their linkages with other networks of mutualists in the ecosystem. Particularly, we aimed to solve the problems of how plant interaction networks are assembled across space, how they can mediate the impact of environmental change on biodiversity, and their consequences for the architecture and robustness of pollination networks.

Our framework is based on ecological systems principles, focusing on the properties of communities and ecosystems emerging from the interactions among species. Particular attention is given to the integration of synecology with natural history knowledge and network theory. Methods include the observation and experimental manipulation of natural communities, computational modelling and quantitative statistics.

The thesis is organised into three independent but complementary manuscripts integrated with one another. In the first chapter we revealed the spatial organisation of plant–plant networks. We discovered a shift from facilitation to competition with increasing spatial scale. Facilitation promotes network cohesivenness and high species richness while competition leads to network collapse. In the second chapter we developed a network robustness model based on trait-environment relationships. We applied this model to a facilitation network and we found that the loss of species varied depending on different environmental change drivers. In the third chapter we introduce a simple field experiment to study the role of plant–plant interactions for the assembly of mutualistic networks. We discovered that plant facilitation scales up to pollinator communities, shaping the architecture and robustness of pollination networks. Moreover, pollination networks created by facilitation were different from the sum of single-network components, a cornerstone of system thinking which was never experimentally proven in ecological networks.

Overall, our results support the idea that plants form collective interaction networks that emerge when positive interactions prevail, like in alpine ecosystems. These positive interaction networks are fundamental for regulating the architecture and functioning of ecological systems.

Zusammenfassung

In alpinen Ökosystemen machen raue Umweltbedingungen den Pflanzen das Leben schwer: Trockenheit, tiefe Temperaturen, nährstoffarme Erde und starke Winde zählen zu den Schwierigkeiten, mit denen die Pflanzen umgehen müssen, um zu überleben und sich fortzupflanzen. Vor zwei Jahrzehnten begannen Ökologen zu berichten, dass benachbarte Pflanzenarten miteinander kooperieren können, um in solch stressreichen Ökosystemen zu überleben. Seither wurden hunderte von Studien durchgeführt, in denen positive Interaktionen (Facilitation) in Pflanzengemeinschaften untersucht wurden. Allerdings haben nur wenige Arbeiten die Interaktionsnetzwerke unter Pflanzenarten und die Konsequenzen dieser Interaktionen für andere Trophieebenen in den Ökosystemen untersucht. Folglich ist bisher unklar, wie sich Pflanzeninteraktionsnetzwerke im Raum bilden, wie sie auf Umweltveränderungen reagieren und wie sie mit mutualistischen Netzwerken verbunden sind.

Das allgemeine Ziel dieser Arbeit ist es, Pflanzeninteraktionsnetzwerke zu studieren, also Pflanzengemeinschaften aus einer Netzwerk-Perspektive anzuschauen. Ziel ist, den Charakter der Interaktionen zwischen Pflanzen, die Netzwerke, die innerhalb Pflanzengemeinschaften aufgebaut werden, und ihre Verbindungen zu anderen Mutualistennetzwerken im Ökosystem zu ermitteln. Insbesondere suchten wir Antworten auf die Fragen, wie Pflanzeninteraktionsnetzwerke sich im Raum bilden, wie sie die Auswirkungen von Umweltveränderungen auf die Biodiversität beeinflussen können, und welche Konsequenzen sie für den Aufbau und die Robustheit von Bestäubungsnetzwerken haben.

Unsere Herangehensweise basiert auf Prinzipien ökologischer Systeme mit Fokus auf den Gemeinschafts- und Ökosystemeigenschaften, die auf Interaktionen zwischen Arten zurückzuführen sind. Besondere Aufmerksamkeit gilt der Integrierung von Synökologie mit naturkundlichem Wissen und Netzwerktheorie. Zu den Methoden gehören die Beobachtung und experimentelle Manipulation natürlicher Gemeinschaften, rechnergestützte Modellierung und quantitative Statistik. Die Dissertation ist in drei unabhängige aber komplementäre, miteinander integrierte Manuskripte gegliedert.

Im ersten Kapitel zeigen wir die räumliche Organisation von Pflanzennetzwerken auf. Wir entdeckten bei zunehmender räumlicher Reichweite eine Verschiebung von Facilitation zu Konkurrenz. Facilitation fördert die Zusammenhaltskraft des Netzwerks sowie Artenreichtum, während Konkurrenz zu Netzwerkkollaps führt.

Im zweiten Kapitel entwickelten wir ein Modell der Netzwerkrobustheit auf der Basis von Merkmal-Umwelt-Beziehungen. Dieses Modell wandten wir auf ein Facilitations-Netzwerk an und stellten dabei fest, dass der Artenverlust je nach Auslöser der Umweltveränderungen unterschiedlich war.

Im dritten Kapitel stellen wir ein einfaches Experiment vor, mit dem wir die Rolle von Pflanzeninteraktionen beim Aufbau mutualistischer Netzwerke untersucht haben. Wir stellten fest, dass sich Pflanzen-Facilitation auf Bestäubergemeinschaften auswirkt und den Aufbau und die Robustheit von Bestäubungsnetzwerken prägt. Zusätzlich unterschieden sich durch Facilitation entstandene Bestäubungsnetzwerke von der Summe der Bestandteile einzelner Netzwerke

– dies ist ein Eckpfeiler des Systemdenkens, der nie experimentell in ökologischen Netzwerken bewiesen wurde.

Insgesamt stützen unsere Resultate die Annahme, dass Pflanzen kollektive Interaktionsnetzwerke bilden, die hervortreten, wenn positive Interaktionen überwiegen – zum Beispiel in alpinen Ökosystemen. Diese positiven Interaktionsnetzwerke sind grundlegend für die Regulierung des Aufbaus und der Funktionsweise Ökologischer Systeme.

Acknowledgments

I am immensely grateful to my supervisor Christian Schöb for giving me the opportunity to be his PhD student. You have been so excellent and bright in mentoring, teaching, supporting, understanding, encouraging, correcting, helping, educating, revising, trusting, criticising, rewarding and stimulating during every single day of my PhD process. Thank you very much.

I am extremely thankful to Bernhard Schmid for directing me and especially for sharing genius intuitions and transmitting his deep, passionate and outstanding scientific knowledge. I have massive gratitude to Jordi Bascompte for his brilliant instructions, sharp comments and fascinating debates.

Many thanks to Richard Michalet for taking part of my committee, providing important ideas. Many thanks to Miguel Fortuna for giving fundamentals suggestions and solutions and for having always positive, encouraging words. Many thanks to Adrián Escudero and Marcelino de la Cruz for the great cooperation and the hospitality received in Madrid. Thanks to all the taxonomists for providing species identification.

A PhD is not only about data analysis, it is rather a matter of passion and love. A gratitude that approaches to infinity is dedicated to Lilian. Without you these pages would not have been the same.

Special thanks to Gian Marco, Dani, Nichi, Elisa and Nayra. Thanks to my office mates Jacqueline, Adele, Enrica, Nadia, Sarah, Yuanyuan, Yanpei, Elvira, Yagmur, Di and Xian, to my colleagues Matthias, Katie, Sam, Janina, Sam, Cam, Mikey, Rich, Terhi, Sofia, Maitane, Marc, Jacqueline, Claudia, to all members of Bernhard's and Jordi's group and to all IEU people with whom I shared thoughts and aperos. Thanks to my nerd flatmate Thanuja, to my mountaineering partner Paul and climbing friends Dan, Lea and Tom.

Heartfelt thanks to my Como buddies Mattia, Poz, Beks, Spiccio, Necci, Lucy, Savi, Kia, Gnacci, Marco, Alex, Marco, Joa and Sale.

Finally, an endless gratitude to mamma Enrica, papi Mauro, sorella Lali, Giò, Ludovica and zia Anna. Grazie.

Introduction

Le temps est venu de nouvelles alliances,
depuis toujours nouées, longtemps méconnues, entre l'historie des hommes,
de leurs sociétés, de leurs savoirs et l'aventure exploratrice de la nature.
— Ilya Prigogine & Isabelle Stengers

The understanding of life represents the core tangle around which human activity has been carried out since ancient history. Modern science has opened a new dialog with nature, based on the integration of theoretical concepts with empirical observations. This science seeks to reveal the global, general truth of the *physis* through the formulation and verification process and the critical discussion of laws and experimental results.

For centuries scientists believed that by breaking up a system in basic units and meticulously measuring every and each part in isolation it would have been possible to deduce the properties of the whole system, hence inferring all its possible future and past states. However, this reductionist approach poses limits at the time of understanding the majority of natural systems, as well as technological and social systems, like ecosystems, cells, the human brain, financial markets, electrical grids and diseases. The common feature of these systems is that they involve many 'components' that interact with each other in a nonlinear way and are consequently organised in an integrated, emergent ensemble. Hence, each component influences the others and it is also influenced by them. As a consequence, by reducing a system in single isolated pieces we also modify the nature and the functionality of its parts. Analogously, natural and ecological systems cannot be understood analysing populations and species in isolation.

The rise of ecological sciences

With the main goal of studying the relationships underlying the living systems, ecology — from Greek *oikos*, "house" and *logia*, "study of"— has developed as the science of "how organisms interact with each other and with their environment" (Bersier, 2007; Levin, 2009). The discipline of ecology emerged from its biogeographic origins at the beginning of the 20th century. Nonetheless, ecological thinking can be traced back to the ancient philosopher Theophrastus (371 BC–287 BC), who classified plants according to their reproduction, locality, size and practical uses in his *Historia Plantarum*.

Ecological principles have developed closely intertwined with other biological disciplines, such as botany and zoology, biogeography and evolution. A father of ecology might be considered the naturalist Alexander von Humboldt (1769–1859), who first studied how form and function of organisms are affected by physical conditions. He is also known for the description of the first global distribution of vegetation according to climate (von Humboldt & Bonpland, 1805).

Since the nineteenth century, ecology has grown around the description of patterns of species and ecosystems across geographical areas as well as the depiction of historical factors limiting species distributions and influencing species diversification. This brought the attention

of pioneer ecologists, like Joseph Grinel and Arthur Tansley, towards the study of species–environment relationships, addressing questions of how environmental factors and habitat properties determine species distributions and ecosystem processes.

The first paradigm in ecology was the idea of plant community as a superorganism (Simberloff, 1980), proposed by Clements in 1905 (Clements, 1905). This concept assumed that communities are organic entities of integrated populations with repeatable spatial patterns. Its further development by the Zurich-Montepellier continental school aimed at classifying communities as Linnaean taxonomic units (Braun-Blanquet, 1932).

The contrasting view of Gleason saw communities as an incoherent continuum where the traits of individual species allow persistence (Gleason, 1926). Later on, the Gleasonian individualistic paradigm had overthrown the Clementsian one. Consequently, analytical ecologists were concerned with the role of environmental selection on organism morphology and physiology for the assembly of communities (Ellenberg, 1953; Elton, 1927; Hutchinson, 1959).

Regardless of their integrity and spatial boundaries, properties of communities became of central interest in ecology. From the 1950s onwards, the discussion was dominated by the deterministic outcome of local species–environment interactions and its integration into models of communities (Verhoef & Morin, 2010). This unidirectional point of view lead to the vision that ecological communities are simply a typological construct, assemblages of species produced only by populations that share adaptation to particular abiotic conditions (Callaway, 2009).

However, organisms are not just passively influenced by abiotic factors, but can actively modify their environment by creating new and destroying former physical conditions (Lewontin, 1983). For instance, corals create reefs, legume plants increase soil fertility, trees reduce light intensity and increase atmospheric humidity. This notion implies that species occurring in an area are not only top-down 'filtered' by the physical environment but can rather bottom-up change the dynamics of ecological processes in fundamental ways. Consequently, organisms are interconnected and interdependent on each other.

The environmental modification by organisms inspired the theories of niche construction (Odling-Smee, 1988), ecosystem engineering (Jones, 1998), foundation species (Ellison *et al.*, 2005), nurse plant syndrome (Shreve, 1931a), contemporary niche theory (Chase & Leibold, 2003) and the integrated community concept (Lortie *et al.*, 2004).

Ecological interactions among living organisms

The history of biodiversity and evolution is fundamentally a history of species interactions (Thompson, 1999).

Competition as a selective force is well established in evolution since its introduction by Darwin in 1859. Similarly, early in the history of ecology theoretical studies of Lotka (1925) and Volterra (1926) and the experimental works of Gause (1934) focused on the oscillations produced by interactions (i.e., predation) between populations.

Despite these premises, the study of interactions among species remained a much less explored ecological field for long time and the question of how species interactions contribute to

Figure 1 The struggle for existence, 1879, George Bouverie Goddard (1832–1886), National Museums Liverpool. Photo credit: Walker Art Gallery.

structuring communities received much less attention compared to the effects of environmental factors. Nevertheless, since the 1960s the study of population dynamics between pairs of species then dominated the arena, with negative interactions such as competition and predation at the centre (Diamond, 1975; Levins, 1968; May, 1973).

These studies boosted the view that ecological communities are the result of tight antagonistic interactions among species. Moreover, central to the understanding of communities is the role of competition coupled with niche theory (Tilman, 1976, 1982). Specifically, intraspecific and interspecific competition associated with the degree of niche overlap between species determine the spatial distribution and the stable species co-occurrence (Chesson, 2000).

However, after almost half-century of research on the role of competition on community organisation (Levin, 1970; Tilman, 1982), no clear, quantitative and predictive theory had emerged yet (Chave, 2009; Levine *et al.*, 2017; Saavedra *et al.*, 2017). Indeed, pairwise competition hardly provides universal rules for communities of many species coexisting (Verhoef & Morin, 2010). Moreover, other processes like spatial dispersion and behaviour have been proven to be fundamental too (Hubbell, 2001; MacArthur & Wilson, 1967). Yet, competition still pervades current ecological principles (Crawley, 1997; Grace & Tilman, 1990; Loreau, 2010a) and the research agenda.

The idea of nature as a competitive race dates back to the late eighteenth century, and it is widespread not only in natural sciences but it is also embedded in many areas of social sciences and arts. In this regard, the painting *The struggle for existence* (Figure 1) by the British artist Goddard (1879) depicting the typical image of nature 'red in tooth and claw' as a deadly fight among wolves is very illustrative. This shows how the idea of competition and fight for survival is deeply-rooted in the human culture.

Science, for just being the cultural product of human activity (Prigogine & Stengers, 1979) is inherently dominated by antagonistic-oriented paradigms. A fly in the face of the majority was that of the Russian naturalist Kropotkin. In his book *Mutual Aid: A Factor of Evolution* (1902) he argued that communities, from social insects to human cities, are arranged according to reciprocal positive interactions among organisms. Unfortunately, his theory did not have enough success among scientists of that time mainly because it was associated to anarchist ideals.

Given the long-standing presence of competitive principles in scientific and human literature, consequently, is not surprising that ecologists have given deep and prolonged attention to the study of negative interactions as competition and predation (Bronstein, 2009b). However, solid evidence indicates that positive interactions are widespread in nature (Nowak & Highfield, 2011). Indeed, mutualism and facilitation are increasingly recognised to be fundamental to patterns and processes within ecological and natural systems (Bascompte & Jordano, 2014; Callaway, 2007).

Plant interactions beyond competition

Research on facilitation is relatively new compared to competition (Bertness & Callaway, 1994; Bruno *et al.*, 2003; Callaway, 2007; Stachowicz, 2001). Facilitation is the positive interaction between two or more species. There is facilitation when a species or a community is experiencing greater colonisation success, recruitment, growth, survival, reproduction, or fitness in the presence of neighbours than in their absence.

Facilitation mechanisms are mainly related to stress decrease, amelioration of microenvironmental conditions and disturbance moderation (Brooker *et al.*, 2008). Consequently, facilitation occurs if the overall improvement results in a positive net outcome for at least one neighbour species.

The first reports of facilitation can be attributed to Shreve (1911; 1931a). In the Sonoran Desert (North America), he described the higher density and diversity of understory plant species in the presence of succulent (like cactus and agave) and sclerophylls (like acacia) plants in comparison to cleared areas where these plant types were absent (Shreve, 1911, 1917). He attributed this pattern to the changes in local physical conditions, particularly to the reduction of aridity and improvement of soil properties (Shreve, 1925). Moreover, he showed the positive effects of both microhabitat ammelioration and root diversity for the germination and survival of understory species (Shreve, 1931b, 1942).

Indeed, the facilitation effect is mainly due to the presence of foundation species (Callaway, 2007; Pugnaire, 2010), also known as nurse plants (McAuliffe, 1984). Foundation species *sensu* Ellison *et al.* (2005) are stress-tolerant species that buffer limiting environmental factors in a way that some other beneficiary species can benefit from the newly created conditions (Bruno *et al.*, 2003; Filazzola & Lortie, 2014; McIntire & Fajardo, 2014).

In ecosystems where harsh and stressful environmental conditions prevail (e.g. low temperature, poor soil), like alpine ecosystems (Callaway *et al.*, 2002; Kikvidze *et al.*, 2005), facilitation

is nowadays considered as a fundamental process (Bruno *et al.*, 2003; Callaway, 2007; He *et al.*, 2013; Pugnaire, 2010).

Worldwide, there is increasing support for the role of facilitation in structuring plant communities (Kikvidze *et al.*, 2015; Michalet *et al.*, 2006; Schöb *et al.*, 2012), maintaining biological diversity (Butterfield *et al.*, 2013; Cavieres *et al.*, 2014; Hacker & Gaines, 1997), mediating biodiversity-ecosystem functioning (Hector *et al.*, 1999; Tilman *et al.*, 1996), increasing food production (Duchene *et al.*, 2017; Schöb *et al.*, 2015), driving natural selection (Ehlers & Thompson, 2004; Michalet *et al.*, 2011) and macroevolution (Valiente-Banuet *et al.*, 2006).

Interestingly, this growing interest for positive, facilitative interactions in plant ecology has been developed in parallel to the study of mutualistic interactions in theoretical ecology. Indeed, research on plant facilitation and mutualistic networks has flourished during the last twenty years (i.e., since the end of 1990s; for comprehensive reviews, see Bascompte & Jordano (2014); Callaway (2007); Fortuna & Bascompte (2008); Pugnaire (2010)). Nevertheless, these two fundamental fields of ecological sciences have rarely been bridged in a research program.

The difference between mutualism and facilitation is that in mutualism both interacting populations benefit while facilitation usually involves the benefits received by beneficiary species regardless of the benefits or costs for the foundation species. Indeed, in mutualism both species should benefit from their interaction, even though the net outcome fluctuates around an equilibrium (Bronstein, 2009a). In facilitation there are benefits for one species while for the other there might be no direct benefit but rather might be costs (Schöb *et al.*, 2014a). Hence, facilitation has been usually seen as a commensalistic interaction (Callaway, 2007; McAuliffe, 1984), but recent evidence supports the view of facilitation as a parasitic interaction (Schöb *et al.*, 2014b). In terms of essentiality, mutualism is mainly obligate while facilitation is facultative. Moreover, facilitation (like competition) usually results from the environmental modification by the facilitator, while mutualism (like predation) requires the physical presence of organisms.

Historically, mutualistic interactions as well as facilitation and competition have been analysed looking at pairwise interactions (Bronstein, 2009b; Loreau, 2010b; Tilman, 1997). Hence, the study of plant interactions has hardly considered networks occurring at the community level.

Ecological networks involving plant species

"Now that science is looking for it, chaos seems to be everywhere" wrote James Gleick (1987) describing the extraordinary success of chaos theory. Analogously, today networks are everywhere. Whether this omnipresence arises from the overloaded use of a new fancy term or rather from the breach opened by complex system theory, which ultimately lead to a novel paradigm transversal to both sciences and humanities, will not be discussed here.

Surely, the fact is that since the end of the twentieth century many systems, like the human brain, food webs, financial markets and electrical grids among others, have been described according to a network model (Cohen & Havlin, 2010). These networks, mathematically modelled as graphs, are defined by nodes (neurones, species, traders and power plants) that are connected

through links (axons, trophic interactions, transactions and transmission lines). The generality and flexibility of such a mathematical tool allowed scientists from disparate fields to reveal commonalities and universal patterns across diverse systems (Newman *et al.*, 2006).

Certainly, network thinking is by no means new to ecology (Bascompte, 2007). Darwin was among the first life scientists recognising the importance of ecological networks (Bersier, 2007) when he described natural communities as a tangled bank of complex species interactions (Montoya *et al.*, 2006).

To understand and synthesise the complexity and stability of trophic interactions between species, the study of food webs has been implemented since the pioneer works of Camerano (1880), Elton (1927), Lindeman (1942) and Paine (1966). Nevertheless, a network approach in ecology has grown popular since the end of the 1990s (Fortuna & Bascompte, 2008). The analysis of 'who eats whom' has provided important insight into the persistence and dynamic of natural ecosystems (McCann, 2011; Williams & Martinez, 2007). Moreover, research on mutualistic networks discovered ecological and evolutionary processes maintaining biodiversity (Bascompte & Jordano, 2014).

Thanks to the recent confluence of ecological and network sciences, a number of new opportunities approaching ecological systems from a complex systems perspective are now open. Yet, networks of interactions within plant communities have been less explored in comparison to other biological and ecological systems.

Three main classes of network types have been used to study plant communities: i) bipartite networks depicting co-occurrence interactions between foundation species and associated beneficiary species (e.g. Burns, 2007; Burns & Zotz, 2010; Verdú *et al.*, 2009; Verdú & Valiente-Banuet, 2008); ii) unipartite networks depicting co-occurrence interactions between species regardless of their ecological role (e.g. Letten *et al.*, 2015; Saiz & Alados, 2011; Saiz *et al.*, 2017), and iii) fully-connected networks assuming competition among all possible species pairs (e.g. Allesina & Levine, 2011; Laird & Schamp, 2006).

From studies in desert ecosystems, we know that foundation species make communities resistant to extinction (Verdú & Valiente-Banuet, 2008) thanks to the nested structure of facilitation networks (Verdú *et al.*, 2010). In a Mediterranean semi-arid ecosystem it has been shown that networks of co-occurring plants are driven by foundation species (Saiz & Alados, 2011) and grazing (Saiz & Alados, 2014). Considering commensal and parasitic interactions, host tree and epiphyte networks in tropical forests showed a nested distribution of interactions (Blick & Burns, 2009; Burns, 2007) that changes with habitat complexity (Sfair *et al.*, 2010) and host traits (Sáyago *et al.*, 2013).

Finally, Allesina & Levine (2011) proposed a theoretical model of a perfectly intransitive (i.e., non-hierarchical) competitive network based on different competitive abilities of species related to environmental limiting factors. They showed that coexistence via intransitive competition (e.g. Species A outcompetes species B, B outcompetes C, and C outcompetes A), which is actually indirect facilitation, is a stabilising niche mechanism and might favour species diversity.

Despite recent advances in analysing networks of interactions among plant species, we are still far from understanding which and how ecological processes generate plant interaction networks, to what extent these processes depend on the environmental context being specific to certain spatial scales, and what is the role of plant networks in regulating the impact of environmental change on biodiversity.

Moreover, how these relationships mediate interactions between plants and other organisms, like their symbionts, hence driving the assembly of ecological networks is still unkwnown.

Scaling up interactions across the ecosystem

Independent from considering community- or network-level interactions and regardless of the nature of these interactions, whether trophic or mutualistic, how interactions within trophic levels scale up to interactions between trophic levels is a fundamental problem still unresolved. Hence, the time is now mature to understand the links between different nested levels of ecosystems.

The pivotal position of facilitation within plant communities has been discussed before. Yet, the role of plant–plant facilitation on other trophic levels and its consequences for ecological networks beyond plant communities is still unknown.

Empirical linkages between the structure of plant and insect communities have been evidenced (Losapio *et al.*, 2016, 2015; Scherber *et al.*, 2010). Moreover, theoretical models support the idea that plants species may support each others pollination (Feldman *et al.*, 2004; Mesgaran *et al.*, 2017). In alpine and desert ecosystems it has been shown that arthropod communities do (Molina-Montenegro *et al.*, 2008; Reid & Lortie, 2012; Ruttan *et al.*, 2016) or do not (Sieber *et al.*, 2011) respond to facilitation by foundation species. Nevertheless, evidence in support of the bottom-up effect of plant interactions on pollination networks is still missing.

Thus, several open questions remain whether interactions among plants control the network of interactions between plants and other organisms in the ecosystem. Particularly, not only the nature of this linkage is unknown, but even the existence of potential cascading, bottom up effects on ecological networks has not been empirically demonstrated yet.

As recently highlighted in Levine *et al.* (2017), it is necessary to integrate single-trophic-level interactions with interactions across trophic levels to make significant progress. Combining these different levels of interactions would unravel the organisation of natural systems across and throughout various scales. This research is the first contribution that fills this gap.

Objective

Summarising, current limitations of standard ecological research are: i) interaction types other than competition are often neglected (e.g. facilitation, mutualism); ii) interaction types are considered in isolation, despite interactions occuring in concert with each other (e.g. pollination and herbivory), iii) interactions are considered at the pairwise level, ignoring that communities and ecosystems are structured by networks of species interactions, iv) interactions are considered

either within trophic levels or between trophic levels, neglecting multiple linkages and feedback effects among different levels in the ecosystem.

This thesis is aimed at a general understanding of ecological processes acting on plant interaction networks, the consequences of network structure for biodiversity, the robustness and collapse of networks under environmental changes and the bottom-up effects of plant interaction networks on mutualistic interactions.

An integrative community-level approach that considers plant networks of different interaction types and involving the scaling across ecosystem levels is fundamental to improve our understanding of ecological patterns and processes and to better infer, hence manage, the responses of biodiversity and ecosystems to ongoing environmental changes.

The thesis is organised into three independent but complementary manuscripts integrated with one another in a common framework. The overall meaning of this thesis, its significance for ecological sciences and societal challenges as well as potential advances are discussed in the conclusion.

1. In the first chapter we describe the spatial dynamic of plant–plant networks in an alpine ecosystem. Bridging spatial pattern with network analysis, our results indicate that positive interactions support the cohesiveness of plant–plant networks while competition leads to network breakdown.

Then, we further wonder how environmental perturbations might affect the network.

2. In the second chapter we develope a novel analytical and conceptual framework to analyse biologically-meaningful cascade extinctions due to environmental change. On the basis of trait-environment relationships, we show that the resistance of networks depends on the type of environmental change driver.

Having revealed the structure and robustness of plant–plant networks, we finally focus on the linkages between these networks and other ecological networks, like plant and pollinator mutualistic networks.

3. With the third chapter we introduce an experimental setting in a Mediterranean alpine ecosystem where we assess the effects of plant facilitation on pollination networks. We discover that the clustering of plants by facilitation affects the interactions between plants and pollinators, with fundamental consequences for the architecture and functioning of pollination networks.

Chapter one

Positive interactions support complex networks

In order to understand ecology properly,
we need to think in terms of relationships, interconnections, patterns, context.
— Fritjof Capra

This chapter is based on the manuscript: Losapio, G., de la Cruz, M., Escudero, A., Schmid, B., & Schöb, C. 2017a Positive interactions support complex networks. *bioRxiv*, 118166. https://doi.org/10.1101/118166.

Ecologists have recognised the effects of biotic interactions on the spatial distribution of living organisms. Yet, the spatial structure of plant interaction networks in real-world ecosystems has remained elusive so far. Using spatial pattern and network analyses, we found that alpine plant communities are organised in spatially variable and complex networks. Specifically, the cohesiveness of complex networks is promoted by short-distance positive plant interactions. At fine spatial scale, where positive mutual interactions prevailed, networks were characterised by a large connected component. With increasing scale, when negative interactions took over, network architecture became more hierarchical with many detached components that show a network collapse. This study highlights the crucial role of positive interactions for maintaining species diversity and the resistance of communities in the face of environmental perturbations.

The nature of biodiversity continues to intrigue biologists because of the complexity of interactions among species in ecosystems. Standard ecological theory assumes that negative interactions between species such as competition are essential to promote stable species coexistence (Allesina & Levine, 2011; Chesson, 2000; Levine *et al.*, 2017; Tilman, 1994). However, recent studies emphasised the importance of positive interactions such as mutualism and facilitation for biodiversity maintenance and ecosystem functioning (Bastolla *et al.*, 2009; Bruno *et al.*, 2003; Cavieres *et al.*, 2014; Wright *et al.*, 2017). Particularly, an impressive amount of studies about networks of mutualistic interactions between plants and animals has increased our understanding of ecological and evolutionary processes shaping communities and ecosystems (Bascompte & Jordano, 2014; Poisot *et al.*, 2016). Conversely, networks of interactions among plants have been less explored. Nevertheless, the existence of interaction networks among multiple plant species has been recently revealed using models of intransitive competition in fully-connected graphs (Allesina & Levine, 2011; Laird & Schamp, 2006; Soliveres *et al.*, 2015), facilitation by keystone species in bipartite networks (Losapio & Schöb, 2017; Verdú & Valiente-Banuet, 2008) and fine scale co-occurrence models for unipartite networks (Letten *et al.*, 2015; Saiz *et al.*, 2014).

Biotic interactions can have consequences on the distribution of organisms and shape the spatial structure of populations and communities. Specifically, competitive interactions can promote fine-scale segregation (Durrett & Levin, 1998; MacArthur & Levins, 1967; Pescador *et al.*, 2014; Tilman, 1994), while facilitative interactions can promote fine-scale aggregation (Bruno *et al.*, 2003; Chacón-Labella *et al.*, 2016; Meron, 2012; Schöb *et al.*, 2008). Consequently, if microhabitat conditions and stochasticity are taken into account it is possible to consider fine-scale spatial aggregation (i.e., significantly positive associations) and spatial segregation (i.e., significantly negative associations) as indicators of facilitation and competition, respectively. Analogously, non significant spatial dependency can indicate neutral net interactions. By considering spatially explicit models, recent studies suggest that the outcome of positive plant interactions may be diffuse, involving many species (Chacón-Labella *et al.*, 2016) and varying with spatial scale (Pescador *et al.*, 2014). Furthermore, increasing evidence high-

lights the importance of indirect interactions for structuring plant communities (Aschehoug & Callaway, 2015; Levine, 1999; Mayfield & Stouffer, 2017; Pages & Michalet, 2003; Schöb *et al.*, 2014b). However, little is known about how plant–plant networks are structured across spatial scales and which network-level factors could maintain species diversity. Directly quantifying the spatial dynamics of plant interaction networks is particularly crucial for understanding how ecosystem processes vary across scales.

To overcome these limitations, we fully mapped a community at the individual-plant level and combined spatial point-pattern with network analyses. We first fitted null models of species distribution and spatial structure for each species. The aim of these null models was to control for niche differences, environmental heterogeneity and stochasticity determining the spatial distribution of each species. Then, we assessed the spatial association among all species to infer species interactions. Although observational approaches are only suggestive regarding the effect of species interactions and other processes, mainly habitat sharing, on spatial association (Soliveres *et al.*, 2015), the observed spatial associations was tested against the expectations of null models of species distribution within the study plot. In this way we accounted for habitat preferences of each individual species. Hence, we assessed wether the observed spatial associations are more or less frequent than expected by hypothetical habitat similarities or differences among species. Finally, we analysed how plant–plant networks changed across spatial scales (Figure 2) and how they were related to plant richness. Because facilitation is known to be a relevant driver in the examined alpine ecosystem (Callaway *et al.*, 2002; Kikvidze *et al.*, 2015; Schöb *et al.*, 2008), we tested the hypothesis that facilitation would support the cohesiveness of plant–plant networks at fine spatial scale, while competition would lead to network disintegration at larger spatial scales.

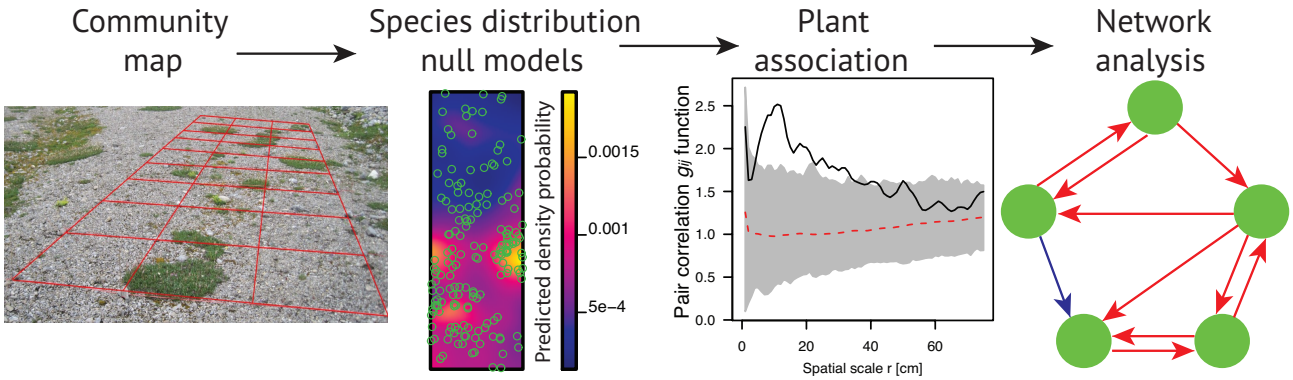

Figure 2 Analytical framework for studying plant–plant networks. A plant community is fully-mapped: for each individual plant, species identity and coordinates are recorded within a spatial grid with a 1 cm accuracy. spatial point pattern analysis is then employed. First, the distribution of each species is analysed (see Appendix one for details). Second, pairwise species associations are estimated after removing the effects of environmental heterogeneity and niche and stochastic processes. Then, species interactions are inferred from spatial association patterns: a positive dependence of species j on species i is assumed to indicate facilitation of species i on species j, a negative dependence is assumed to indicate competition, and no association is assumed to indicate net neutral interactions. Finally, network analysis is used to reveal the structural properties of the networks across spatial scales.

Results

Shifts of plant–plant interactions across space

A total of 983 interactions were detected across spatial scales among the 19 species. Positive interactions were 592 (60.2%), of which 282 (47.6%) were mutual and 310 (52.4%) were non-mutual. Negative interactions were 391 (39.8%), of which 128 were mutual (32.7%) and 263 were non-mutual (67.3%). No negative–positive interactions were observed. The ratio of positive to negative interactions decreased with increasing spatial scale from 1–75 cm ($\beta = -10.294$, $\beta^2 = 2.671$, $\beta^3 = -2.417$, $p = 0.0001$, $R^2 = 0.607$; Figure 3a), along with a decrease of the ratio of mutual to non-mutual interactions ($\beta = -10.328$, $\beta^2 = 6.656$, $\beta^3 = 3.606$, $p = 0.0005$; $R^2 = 0.590$; Figure 3b). This shift from positive to negative interactions went along with a decrease of species richness across spatial scales (Fig. S12). In particular, the richness of interacting plant species increased as the relative amount of positive over negative interactions increased ($\beta = 11.798$, $\beta^2 = -1.800$, $\beta^3 = 4.469$, $p = 0.0019$, $R^2 = 0.270$; Fig. S13).

Effects of interaction type

Positive and mutual interactions had a positive effect on the total number of interactions L ($p = 0.0006$, $R^2 = 0.665$; Tab. S3.), while only positive, but not negative, interactions had a positive effect on interacting species richness S ($p = 0.0004$, $R^2 = 0.630$). Thus, there was a decrease in the number of interactions associated with a shift in the predominant interaction type from mutual and positive to non-mutual and negative with increasing spatial scale ($p = 0.0001$, $R^2 = 0.607$, Fig. 2c-d, Tab. S3).

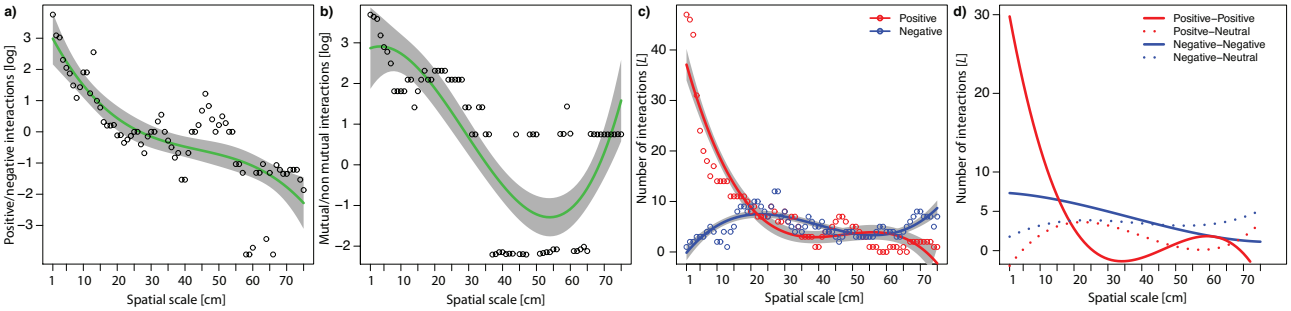

Figure 3 Log ratio between positive and negative interactions **a)**, mutual and non-mutual interactions **b)**, total positive and negative interactions **c)** and total mutual and non-mutual interactions **d)** across spatial scales. Red and blue lines indicate positive and negative interactions, respectively; in **d)**, solid and dashed lines indicate mutual and non-mutual interactions, respectively. Predicted lines (i.e. Non-linear regression model with the third degree polynomial function of scale as predictor and an autoregressive covariance structure) and 95% CI shown. In **d)** data points and CI omitted for clarity.

Global network architecture

Network clustering gradually decreased within the first 30 cm and then abruptly dropped to 0 with further distance ($\beta = -0.970$, $\beta^2 = 0.348$, $\beta^3 = -0.062$, $p < 0.0001$, $R^2 = 0.558$; Figure 4). All interaction-type combinations had significant effects on network clustering (Tab.

S4). However, considering their effect size, positive mutual interactions best explained network clustering ($\beta = 0.044$, $r^2 = 0.361$, $p < 0.0001$), followed by positive non-mutual interactions ($\beta = 0.065$, $r^2 = 0.225$, $p = 0.0018$), whereas negative mutual ($\beta = 0.026$, $r^2 = 0.096$, $p = 0.0247$) and non-mutual ($\beta = -0.089$, $r^2 = 0.117$, $p = 0.0139$) interactions had weaker effects. This indicates that positive mutual interactions among plant s were associated with higher clustering among neighbouring plants.

There were connected components across all scales, but their size decreased with increasing scale ($\beta = -22.530$, $\beta^2 = 6.343$, $\beta^3 = 4.270$, $p < 0.0001$, $R^2 = 0.599$) up to about 55 cm (Figure 4b). Positive mutual and non-mutual interactions and negative non-mutual interactions had significant positive effects on the size of the largest connected component R (Tab. S4). Again, positive mutual interactions ($\beta = 1.189$, $r^2 = 0.504$, $p < 0.001$) and positive non-mutual interactions ($\beta = 2.090$, $r^2 = 0.383$, $p < 0.0001$) best explained variation in R, followed by negative non-mutual interactions ($\beta = 3.810$, $r^2 = 0.249$, $p < 0.0001$). Species proximity decreased with increasing spatial scale (Figure 4c). This indicates a network collapse with increasing spatial scale.

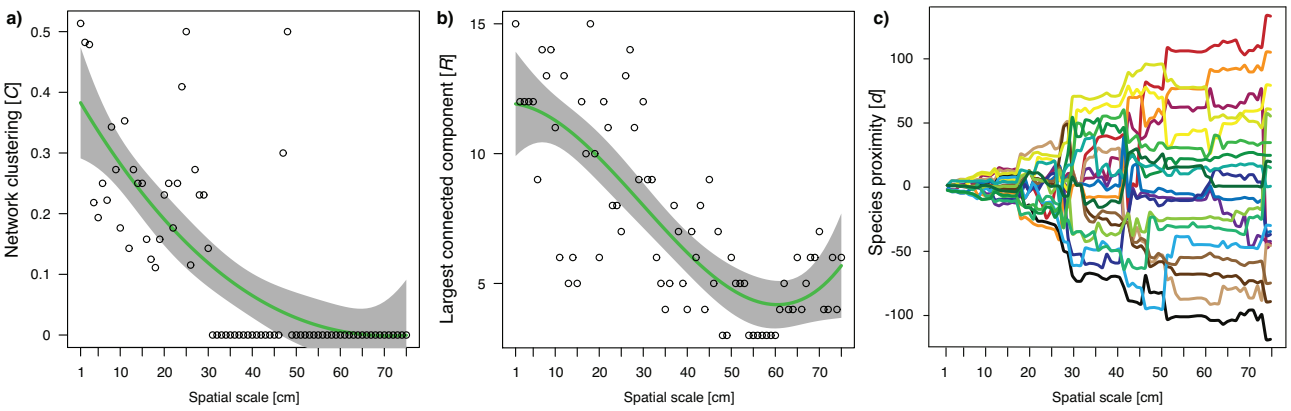

Figure 4 Network transitivity C **a)**, size of the largest connected component R **b)** and species proximity **c)** across spatial scales. Transitivity, measured by the clustering coefficient C (Watts & Strogatz, 1998), indicates local cohesiveness of a group of nodes (i.e. Species). The size of the largest connected component R is the maximum number of interconnected species within a network (Molloy & Reed, 1995). A change in the size of the largest connected component provides basic information about the growth of a network. Predicted lines and 95% CI shown. species proximity calculated on the basis of relative geodesic distance (Bender-deMoll, 2016). Each horizontal spline corresponds to a plant species and vertical proximities are proportional to the number of interactions connecting them. The larger the proximity, the higher the fragmentation of the network.

Discussion

Our study highlights the role of positive interactions among plant species for the architecture of complex plant–plant networks. After controlling for niche differences and environmental heterogeneity, we found that facilitation prevailed at spatial scales up to 25 cm, while competition became dominant at spatial scales larger than 50 cm in our alpine ecosystem. This shift from facilitation to competition with increasing distance was coupled with a de-structuring of plant–plant networks, which was ultimately associated with less interacting species. These results support our hypothesis that plant–plant networks change across spatial scales (Figure 5).

Furthermore, they suggest that positive plant interactions could be pivotal in the network organisation of species-rich patches in this stressful, fragmented ecosystem. In summary, at fine spatial scales, positive interactions promoted the cohesiveness of plant–plant networks with high clustering and large connected components. Conversely, at larger spatial scales, networks became more hierarchical and less cohesive in parallel with a relative increase in competitive interactions. Because network complexity may increase ecosystem stability (Solé & Bascompte, 2006), positive plant interactions may promote plant species richness and ecosystem stability, similarly to obligate plant–animal mutualistic interactions (Bastolla *et al.*, 2009).

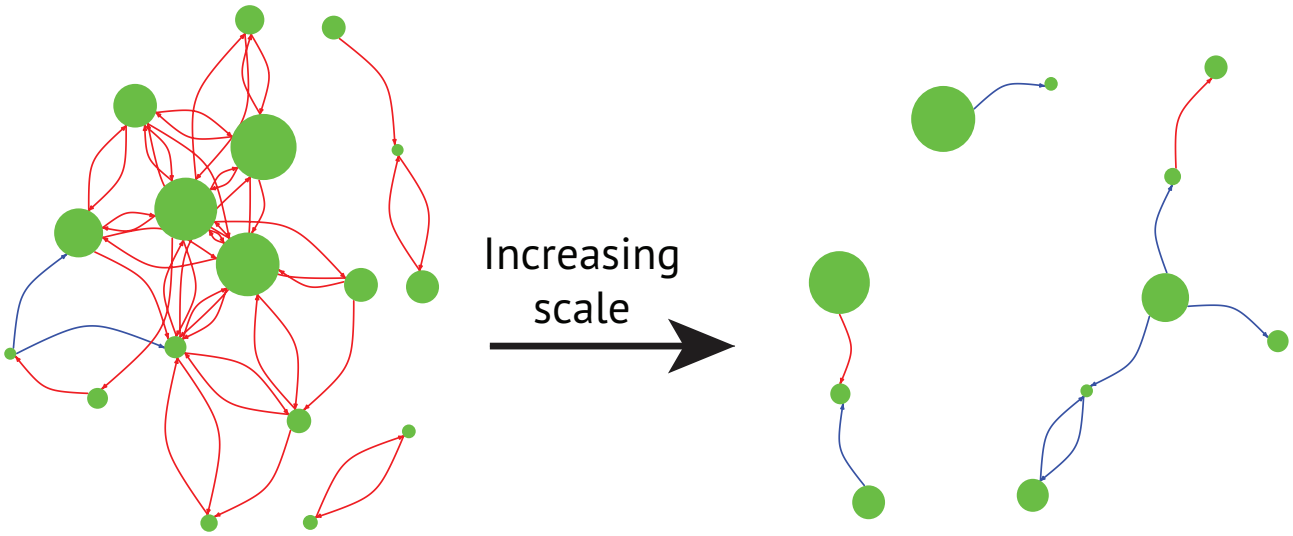

Figure 5 At fine spatial scale (left, 2 cm) positive facilitative interactions (red arrows) build up a network with high transitivity, i.e. high cohesiveness. With increasing scale (right, 50 cm), negative competitive interactions (blue arrows) predominate and the network becomes more disconnected. The size of the nodes (green dots) is proportional to relative species abundance (See Fig. S10 and the online video for the network at every centimetre).

The spatial scale of plant interactions

Theoretical and empirical studies indicate that the emergence of spatial patterns is due to two main classes of mechanisms of ecological self-organisation (Kéfi *et al.*, 2007; Meron, 2012; Rietkerk *et al.*, 2004; Solé & Bascompte, 2006; Tarnita *et al.*, 2017). The first process considers the role of positive scale-dependent feedbacks between biomass and resources. The second process recognises the role of species as ecosystem engineers and their intraspecific competition. At short distance, plants may increase resource availability, hence ameliorating growth conditions in environments with high abiotic stress as our alpine ecosystem (Kikvidze *et al.*, 2015; Schöb *et al.*, 2012). This means that the more plants the stronger the stress amelioration by facilitation can be (Meron, 2012). Such positive feedback mechanism may explain why facilitation prevailed at the very close proximity to plants, i.e. within vegetation patches. Furthermore, water transport within a patch increases its growth while it inhibits the growth of neighbouring patches. Hence within-patch facilitation may depend on the possibility to exploit resources within and around the patch, thereby leading to between-patch competition (Meron, 2012). In our case, the importance of competition varied relatively less across scales. Therefore, we

suggest that the prevalence of competitive interspecific interactions at larger distances may be associated to resource dynamics between local patches compared to within local patches (Meron, 2012; Rietkerk *et al.*, 2004; Tilman, 1994). In summary, facilitation may be scale-dependent, whereas competition may be rather constant across space in our fragmented alpine ecosystem.

In addition to these two processes, we postulate here that positive interspecific interactions may be associated with cohesive networks and with the richness of species participating in these networks (Fig. S15). This means that positive interspecific interactions may promote the establishment of more links among different neighbour species. Such effect may result in a facilitation cascade (Stachowicz, 2001) according to an autocatalytic process (Meron, 2012; Rietkerk *et al.*, 2004; Solé & Bascompte, 2006) and similarly to the emergence of cooperation in public goods games (Rand *et al.*, 2009). In other words, the presence of positive interactions among neighbouring, diverse plants could be associated with the prevalence of the same positive interactions in the network in plants vicinity. Conversely, at larger distance, the prevalence of negative interactions may reduce the likelihood of species occurring in the network. Ultimately, this may potentially lead to local patches of unexpectedly high species richness characterised by diffuse facilitation (Chacón-Labella *et al.*, 2016).

The spatial dynamics of plant–plant networks

Networks show a high clustering when the number of interactions among neighbours is large relative to the number of species (Watts & Strogatz, 1998). The decreasing clustering with increasing scale implies that a transition from a cohesive to a hierarchical organisation of networks occurred in our alpine ecosystem. This shift was nonlinear, but gradual until reaching a threshold at 30 cm, beyond which a sudden, critical transition occurred and clustering rapidly approached zero. This pattern concurs with expectations of the behaviour of an (eco)system approaching a tipping point (Solé & Bascompte, 2006), highlighting the probable presence of a collapse of the architecture of plant–plant networks. The network collapse could be coupled with the facilitation–competition shift observed across spatial scale in this fragmented system. Potential mechanisms leading to such a shift can be related to previously described positive scale-dependent feedbacks, where positive interactions prevail within patches and negative interactions at larger scale (Meron, 2012). Coupled to this process there are the positive effects that ecosystem engineers, like *Dryas octopetala* in our system, have on other species (Tarnita *et al.*, 2017), mainly through the decrease of stress and the amelioration of growth conditions (Klanderud, 2005).

The size of the largest connected components in our networks decreased with increasing spatial scale to half the size at 30 cm and to one-fifth at 55 cm. Again, this reduction in component size was associated with a reduction in positive interactions. In line with this result, we also found a higher species proximity in the network at fine spatial scale where positive interactions were predominant. This indicates that species closely interact at fine scale while were less closed within the network with increasing scale and negative interactions. Accordingly,

the number of cliques (Fig. S14) decreased with increasing spatial scales, indicating network breakdown at its sub-structure level. Taken together, these results suggest a breakdown of the largest connected components with increasing spatial scale, as species tend to segregate into many detached components once positive interactions wane.

Our study is one of the first attempts to analyse the spatial structure of plant–plant networks across scales. We are aware that new questions are now arising. Observational studies such as the present one may suggest potential mechanisms underpinning spatial patterns of species interactions. Nevertheless, with our approach we first controlled for variation in niche differences and environmental heterogeneity before calculating spatial association and then inferring plant–plant interactions (Chacón-Labella *et al.*, 2016; Pescador *et al.*, 2014; Wiegand & Moloney, 2014). Moreover, it should be noted that what we observed as facilitation between two species might also be apparent facilitation, in which the two species are both facilitated by a third one.

Future experimental studies controlling for differences in demographic stochasticity (e.g. dispersal limitation) and niche processes (e.g. species-specific resource limitation) would be necessary to test the causality of the observed correlations between positive and negative plant–plant interactions with network architecture. At the same time, further theoretical research should accompany such experimental work to better predict network stability under different environmental conditions.

We conclude that positive interactions exceed negative ones at fine spatial scales. The resulting increase in network cohesiveness is best supported by the spread of positive interactions among neighbouring plants within the local network in a way that facilitation begets facilitation.

Methods

Study area and sampling design

An observational study was performed in a sparsely-vegetated alpine ecosystem (Swiss Alps, 2300 m a.s.l., Lat 46.39995°N, Long 7.58224°E, Fig. S1) characterised by patches of the prostate dwarf-shrub *Dryas octopetala* L. (Rosaceae). The plant community was fully mapped with a 1 cm accuracy during August 2015 within a 9 x 3 m rectangular grid (Fig. S2). For each individual plant (i.e., ramet) we recorded: species identity, coordinates of rooting point (x and y) and a set of functional traits (width, height, number of leaves, leaf dry mass) relevant for resource use and competitive ability (Díaz *et al.*, 2016). In total, 2154 individuals belonging to 29 species were recorded (Tab. S1). Species richness reached an asymptote in the accumulation curve (Fig. S3), suggesting that a representative area with the entire species pool of this plant community type was sampled. We focused on the 19 species that had more than 10 individuals in order to minimise analytical bias. Fine-scale spatial heterogeneity of soil properties was quantified by determining soil gravel content, soil water content and soil C/N ratio with one composite sample in each 1 m^2 and beneath each *Dryas* patch (see Appendix one for details).

Spatial pattern analysis and plant interactions

To detect the statistical association between species and infer plant interactions we employed spatial point pattern analysis based on second-order statistics (Baddeley *et al.*, 2015; Diggle, 2003; Ripley, 1981; Wiegand & Moloney, 2014) assuming that spatial patterns could inform about interactions (Kéfi *et al.*, 2007; Meron, 2012; Rietkerk *et al.*, 2004; Saiz *et al.*, 2014; Schöb *et al.*, 2008; Solé & Bascompte, 2006; Verdú & Valiente-Banuet, 2008) after accounting for other processes (Baddeley *et al.*, 2015; Diggle, 2003; Wiegand & Moloney, 2014). The scale of analysis was varied from 1 cm to 75 cm.

First, we describe the spatial distribution of each species. To identify the effects of environmental heterogeneity, niche differences and stochasticity on the species occurrence probability, we fitted different models of spatial distribution within the plot based on species traits, soil properties and stochastic processes for each species. The model with the best goodness of fit was selected as the null model to later test spatial association between species (see Appendix one for details).

Second, we determined interspecific spatial associations. We carried out bivariate point pattern analyses for all species pairs to assess the existence of spatial associations between species after accounting for their niche differences and the microenvironmental conditions. We assume that fine-scale spatial segregation and fine-scale spatial aggregation are indicators of competition (Durrett & Levin, 1998; MacArthur & Levins, 1967; Pescador *et al.*, 2014; Tilman, 1994) and facilitation (Bruno *et al.*, 2003; Chacón-Labella *et al.*, 2016; Meron, 2012; Schöb *et al.*, 2008), respectively. Species association was calculated using the inhomogeneous cross-type pair correlation function $g_{ij}(r)$ (Wiegand & Moloney, 2014). Given the expected number of points (i.e. Individual plants) of species j at a distance r from an arbitrary point of species i (Fig. S4), the probability $p(r)$ of finding two points i and j separated by a distance r is equal to $p(r) = \lambda_i(x)\lambda_j(j)g_{ij}(r)\ \mathrm{d}x\ \mathrm{d}y$, where $\lambda_i(x)$ and $\lambda_j(j)$ are the estimated intensity functions of each species (see Tab. S2). Values of $g_{ij}(r) > 1$ indicate that there are, on average, more individuals of species j at a distance r from species i than expected by chance. Conversely, values of $g_{ij}(r) < 1$ indicate that species j is more segregated from species i than expected by chance. When $g_{ij} \approx 1$ the spatial dependency of species j on species i cannot explain more than what we would expect by chance, i.e., given each species' distribution.

In order to statistically determine whether an observed pattern was significantly different from what could be expected by chance, Monte Carlo simulation of a realisation of the $g_{ij}(r)$ function at each scale (for r from 1–75 cm with 1 cm steps) was used to generate simulated distributions from the null hypothesis of independence of species j with respect to species i. A total of 199 MC simulations were performed at each scale. The fifth-lowest and the fifth-highest simulated values at each r were used to build 95% confidence envelopes around the mean predictions (Baddeley *et al.*, 2015; Diggle, 2003). Thus, at a given scale r, an empirical $\hat{g}_{ij}(r)$ function higher than the confidence envelope indicates significant positive dependence of species j on species i, while the converse indicates significant negative dependence (Fig. S8, Fig. S9). When $\hat{g}_{ij}(r)$ lies within the MC confidence envelope, neutral association cannot be

rejected. Because first order constraints on the distributions of each species are controlled (i.e. Microsite heterogeneity, niche and stochastic determinants, see Appendix one), the obtained positive and negative dependences might result from non-random plant–plant interactions (Kéfi *et al.*, 2007; Rietkerk *et al.*, 2004; Tilman, 1994; Wiegand & Moloney, 2014). Finally, with this approach we could detect the spatial scales at which such interactions are operating according to the corresponding spatial signals.

Network analysis

Network analysis was employed to identify the web of plant–plant interactions and to assess how network architecture may promote species coexistence and maintain species richness. At each scale we built a unipartite directed network $G = (V, E)$ composed of $V = 19$ plant species and $E \subseteq V_i \times V_j$ significant directional interactions (i.e., distinguishably E_{ij} and E_{ji}), for a total of 75 networks and 983 species interactions (Fig. S10). Each network G was represented by an adjacency matrix M composed of 19 rows and 19 columns describing interactions among plant species.

Species interactions $E_{ij}(r)$ are described by directed ternary links such that

$$E_{ij}(r) = \begin{cases} 1 & \text{for facilitation} & \text{if } \hat{g}_{ij}(r) > g_{theo}(r) + 95\% \text{ CI} \\ \text{-1} & \text{for competition} & \text{if } \hat{g}_{ij}(r) < g_{theo}(r) - 95\% \text{ CI} \\ 0 & \text{for neutral} & \text{else } (i,j) \notin E \end{cases}$$

To reveal changes in local plant–plant interactions across scales, for each network we calculated the total number of interactions E, the number of species S with at least one interaction ($S < V$), and the number of pairwise interactions for each bidirectional interaction type, i.e., positive mutual (facilitation–facilitation), positive non-mutual (facilitation–neutral), negative mutual (competition–competition), negative non-mutual (competition–neutral) and negative–positive (facilitation–competition) (Fig. S11).

Network architecture was analysed using the clustering coefficient C (Watts & Strogatz, 1998). C tests if two or more species linked to another species are also interacting with each other, measures the local cohesiveness of a group of species and indicates the neighbourhood interaction density as well as the hierarchy and interconnection of a community (Fig. S11). C is defined as the probability that neighbouring nodes (i.e., all plant species connected to a plant species i) of a plant species i are linked to each other. In other words, C for any node i is the fraction of linked neighbours of i, such that $C = N^{-1} \sum_{i=1}^{N} (s_i(k_i - 1))^{-1}$, where s_i is the sum of links present among neighbouring nodes for each node i, and k_i is the degree (i.e., the number of neighbours) of node i. Thus, the higher the clustering, the more the neighbours are connected to each other and the higher the cohesiveness.

To reveal network growth and collapse across spatial scales, we calculated the size of the largest connected component R. A connected component of a network is a subset of nodes reachable from every node within it (Molloy & Reed, 1995). In other words, the size of R is equal to the maximum number of species consecutively linked within a network (Fig. S11). The

change in the size of R provides basic information about network development and collapse. Hence, the presence of connected components and the change in their size R can be used to characterise the robustness of ecological communities.

To reveal network collapse, we calculated species proximity on the basis of relative geodesic distance, i.e. Considering nodes positioned on a plane alike (Bender-deMoll, 2016). The larger the proximity, the larger the network-based distance among species, the higher the fragmentation of the network.

Statistical analyses

We first analysed the changes in plant–plant interactions across spatial scales and then we tested the relationships between such changes and network architecture.

We used regression models to relate the response of i) the total number of interactions E and ii) the interacting species richness S to the ratio between positive and negative interactions, the ratio between mutual and non-mutual interactions and their interactions (fixed effects with third degree polynomials for each ratio, i.e., $r + r^2 + r^3$). Besides, we previously tested with the same approach if the ratio between positive and negative interactions and the ratio between mutual and non-mutual interactions changed across scale (i.e. $S + s^2 + s^3$).

Then, to determine bottom-up effects of local plant–plant interactions on network architecture, we used regression models to test the effects of pairwise interaction combinations (i.e. Number of positive–positive, positive–neutral, negative–negative, negative–neutral, negative–positive interactions as fixed effects) on i) the network transitivity C, and on ii) the size of the largest connected component R. By using the absolute number of each interaction-type combination as independent variable we accounted for changes in the total number of interactions across scales. To quantify the importance (i.e. Effect size) of the different interaction types and spatial scale, we used the partial r^2, i.e. The proportion of variation that can be explained by each explanatory variable, calculated as $r^2_{y,xi|xk} = \frac{SSE_{(reduced)} - SSE(full)}{SSE(reduced)}$, where the error sum of squares SSE (i.e., residuals) were compared between reduced models excluding only one interaction type x_i and the full model containing all interaction types x_k.

We accounted for spatial autocorrelation across scales by including an autoregressive covariance structure ($AR_{(1)}\sigma_{ij} = \sigma^2\rho^{|i-j|}$) in all models (Pinheiro *et al.*, 2016).

All analyses were done in R 3.3.0 (R Core Team, 2017), using *spatstat* (Baddeley *et al.*, 2015) and *ecespa* (De la Cruz, 2008) for spatial pattern analysis, *igraph* (Csárdi & Nepusz, 2006) for network analysis and *nmle* (Pinheiro *et al.*, 2016) for statistical analysis.

Data availability

The data that support the findings of this study will be deposited in Dryad repository.

Acknowledgments

This study was financially supported by the Swiss National Science foundation (PZ00P3_148261) to CS and partially by the Spanish Ministry of Economy and Competitiveness under the project ROOTS (CGL2015.66809-P) to AE. We thank L. Dutoit and D. Trujillo for their help with data collection in the field. We thank J. Bascompte and M. Fortuna for their fruitful discussions and commenting on an early version of this manuscript.

Author contributions

GL and CS designed the study, GL collected data and analysed them, MC provided new analytical methods, all authors discussed data analysis, commented the results and edited the manuscript. All authors are included in the author list and agree with its order and they are aware the manuscript has been submitted.

Competing interests

The authors declare no competing financial interests.

Supplementary Information

Supplementary methods, figures, tables, data and R scripts accompany this paper.

Chapter two

Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes

Cooperation underpins innovation, it is the architect of creativity.
— Martin Nowak

This chapter is based on the manuscript: Losapio, G. & Schöb, C. (2017). Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. *Functional Ecology*, 31, 1145-1152. https://doi.org/10.1111/1365-2435.12839

Functional Ecology

British Ecological Society

Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes

Gianalberto Losapio & Christian Schöb

In Mediterranean alpine ecosystems, harsh conditions make plants' lives difficult: drought, low temperature, poor soil and strong winds are some of the problems plants have to cope with to survive and reproduce. Two decades ago, ecologists started to report that plants can cooperate with neighbouring plants to survive in such a harsh environment. Since then, hundreds of studies were subsequently conducted, but few of these described the network of interacting plant species, despite our knowledge that natural plant communities are organized in such interaction networks. Thus, it remains unclear whether such plant interaction networks differ in their resistance against different environmental changes. Here we assessed the susceptibility of a network of interacting plants to simulated increases in drought, temperature and drought, and nitrogen deposition.

We combined observational data from an alpine vegetation in the Sierra Nevada Mountains (Spain) with computer simulations to explore the probabilities of these environmental changes causing species extinctions, either due to environmental conditions becoming unsuitable or due to the loss of their microhabitat. We found that plant interaction networks' responses, and the extinctions of species, depended on the type of environmental change. In particular, the studied plant community was most resistant against species losses when drought increased. However, it was least resistant, and experienced early and heavy species losses, when nutrient pollution increased. We further showed that the higher network resistance against increasing drought was due to drought-tolerant species that facilitated the survival of many other plant species.

Sampling plot of plant species in the Sierra Nevada Mountains (Spain) at 2725 m a.s.l. The grass Festuca indigesta Boiss. (Poaceae) is supporting other plant species to survival in this stressful environment. © Christian Schöb.

This study suggests that the fate of species and communities with the on-going global environmental changes will depend on the main driver of environmental change and how this might affect the network of interacting species. Consequently, knowledge about species interaction networks in natural communities could improve our understanding of how ecosystems will respond to global changes, which in turn may help to improve current conservation and restoration practices.

Plant interactions are fundamental processes for structuring plant communities and are an important mechanism governing the response of plant species and communities to environmental changes. Thus, understanding the role played by the interaction network in modulating the impact of environmental changes on plant community composition and diversity is crucial. Here, we aimed to develop a new analytical and conceptual framework to evaluate the responses of plant communities to environmental changes. This framework uses functional traits as sensitivity measures for simulated environmental changes and assesses the consequences of microhabitat loss. We show here its application to an alpine plant community where we recorded functional traits (specific leaf area [SLA] and leaf dry matter content [LDMC) of all plants associated with three foundation species or the surrounding open areas. We then simulated primary species loss based on different scenarios of environmental change and explored community persistence to the loss of foundation species. Generally, plant community responses differed among environmental change scenarios. In a scenario of increasing drought alone (i.e., species with lower LDMC were lost first) or increasing drought with increasing temperature (i.e. Species with lower LDMC and higher SLA were lost first), the plant community resisted because drought-tolerant foundation species tolerated those deteriorating conditions. However, in scenarios with increasing nitrogen input (i.e., species having lower SLA were lost earlier), foundation species accelerated species loss due to their early primary extinctions and the corresponding secondary extinctions of species associated to their microhabitat. The resistance of a plant community depends on the driver of environmental change, meaning that the prediction of the fate of this system is depending on the knowledge of the main driver of environmental change. Our framework provides a mechanistic understanding of an ecosystem response to such environmental changes thanks to the integration of biology-informed criteria of species sensitivities to environmental factors into a network of interacting species.

Introduction

There is evidence that global environmental changes are affecting the stability of ecosystems (Hautier *et al.*, 2015) causing a worldwide decline in biodiversity (Cardinale *et al.*, 2012) with unprecedented high extinction rates (Pimm *et al.*, 2014). However, the consequences of environmental changes for biotic interactions are much less known (Bascompte & Jordano, 2014; Michalet *et al.*, 2014), despite the importance of species interactions for mediating species tolerance and community persistence under environmental changes (Fortuna & Bascompte, 2006; Ives & Cardinale, 2004; Memmott *et al.*, 2007; Saavedra *et al.*, 2013).

Plant–plant interactions are fundamental processes for structuring plant communities (Klanderud, 2005; Michalet *et al.*, 2015). In alpine ecosystems, where harsh environmental conditions prevail (e.g. low temperature, poor soil), stress-tolerant foundation species (i.e., species that influence community structure and ecosystem processes, *sensu* Ellison *et al.* (2005)) often promote species survival and growth, and community-level diversity, through creation of unique microhabitats (Cavieres *et al.*, 2014). These effects of foundation species have been attributed to facilitative effects on their co-occurring plant species, for example through the ability of foun-

dation species to ameliorate micro-environmental conditions (Butterfield & Callaway, 2013; McIntire & Fajardo, 2014; Schöb *et al.*, 2012).

Thus, understanding the role played by microhabitats created by foundation species in sustaining biodiversity with a changing climate is crucial (Brooker, 2006; Ellison *et al.*, 2005), especially in Mediterranean alpine ecosystems, where facilitation by foundation species is particularly relevant for plant community diversity (Michalet *et al.*, 2014; Pistón *et al.*, 2016; Schöb *et al.*, 2013a). Consequently, plant–plant interactions matter, but our tests of their importance are generally pairwise. A holistic community-level approach that considers networks of interacting species would be useful and might improve our understanding of species and community responses to environmental changes. However, such a network approach has hardly been employed so far (but see Allesina & Levine (2011); Saiz & Alados (2011); Verdú & Valiente-Banuet (2008)).

To investigate the resistance of a community to environmental perturbations, a common approach is to perform random extinctions or target extinctions that eliminate the most and the least connected species of an interaction network first (Dunne *et al.*, 2002; Memmott *et al.*, 2004; Solé & Montoya, 2001; Verdú & Valiente-Banuet, 2008). However, such an approach does not consider species sensitivity to specific environmental changes (Curtsdotter *et al.*, 2011; Ives & Cardinale, 2004). Functional traits can offer such a biology-informed, mechanistic link between prevailing environmental conditions and the likelihood of species survival (Garnier *et al.*, 2016; McGill *et al.*, 2006). Indeed, by capturing essential aspects of species ecophysiology, functional traits determine the sensitivity of plants to biotic and abiotic factors (Ackerly, 2004; Butterfield & Callaway, 2013; Grime, 2001; Schöb *et al.*, 2012; Westoby *et al.*, 2002). Consequently, traits predispose plant species to extinction under certain kinds of environmental changes (Cardinale *et al.*, 2012).

In this study we present a new analytical and conceptual framework to simulate plant community persistence against environmental perturbations, showing its application to a Mediterranean alpine plant community dominated by three foundation species. We characterise the plant–plant interaction network and explore the consequences of foundation species loss for biodiversity using functional traits as a biological criterion of species' sensitivity to environmental changes. We then estimate the loss of species that is caused by the primary loss of microhabitats created by foundation species (i.e., secondary extinctions *sensu* Brodie *et al.* (2014). We hypothesised that community persistence and the rate of species loss varied among environmental change scenarios, as would the role of foundation species in modulating the species loss.

Materials and methods

Study area

The study was performed in the Sierra Nevada Mountains (Spain, 2725 m a.s.l., 37.08134°N, -3.38127°E), where the importance of positive plant interactions for community structure and

diversity is well documented (Pistón *et al.*, 2016; Schöb *et al.*, 2013a,b, 2012, 2014b). The site was a relatively homogeneous 0.5 ha plot, with a patchy plant community dominated by three foundation species: the cushion-forming species *Arenaria tetraquetra* spp. *amabilis* (Bory) H. Lindb. Fil. (Caryophyllaceae) and *Plantago holosteum* Scop. (Plantaginaceae), and the tussock grass *Festuca indigesta* Boiss. (Poaceae).

At the closest weather station in Pradollano (2500 m a.s.l.; 37.08333°N, -3.38333°E) mean growing season (May–September) temperature is 13.8°C (average min 6.2°C, average max 21.5°C) and mean annual precipitation is 690 mm, with a dry summer period during July and August (http://es.climate-data.org). The habitat belongs to the oro-Mediterranean acidic grassland type characterised by low-productivity, siliceous gravel substrate with poorly developed soils and generally low soil organic matter and water content (Schöb *et al.*, 2012).

The examined foundation species are known to provide positive effects on some other plant species in the study area, mainly through provision of higher soil organic matter and soil water compared to bare ground (i.e. open) areas (Schöb *et al.*, 2013b, 2012). This positive, facilitative effect was demonstrated by a better plant water status and higher reproductive output of subordinate species associated to foundation species (Schöb *et al.*, 2014b), indicating the dependency of subordinate species on microhabitats created by foundation species for their survival and reproduction.

Sampling was performed within the canopy area of 40 individuals of each of the three foundation species and in 10 open areas (hereafter, we refer to these samples as plots and to the each of the three foundation species and the open areas as different microhabitats, respectively).We identified all individuals of plant species in each plot and subsequently refer to them as subordinate plant species either occurring within the canopy of foundation species or in the open microhabitat (see Appendix two).

As plant–plant interactions are local processes acting at fine spatial scale, sampling was performed at a centimetre scale, consistent with previous studies in the study area that inferred plant interactions from spatial patterns (Pistón *et al.*, 2016; Schöb *et al.*, 2013a,b, 2012, 2014b). Plot size was equal to the foundation species canopy size: 168 (8-406) cm^2 (mean (min-max)) for *Arenaria*;149 (3-638) cm^2 for *Plantago*; 241 (<1-1'018) cm^2 for *Festuca*. In the open we sampled circular plots (27.6 cm diameter or 598 cm^2) that were randomly placed in gaps between foundation species

Trait–environment relationships

We used two functional traits with a known sensitivity to environmental conditions and related to resource use strategies: specific leaf area (SLA) and leaf dry matter content (LDMC). SLA increases with soil nutrient availability (Ordoñez *et al.*, 2009) and is related to photosynthesis and respiration (Garnier *et al.*, 2016). LDMC increases with drought (Ackerly, 2004), where physically robust species have high LDMC with high carbon-construction costs (Westoby *et al.*, 2002). Along this leaf economics spectrum (Díaz *et al.*, 2016), species with high LDMC and low SLA have lower photosynthetic rates and slower return on investment, indicating a conservative

growth strategy and high drought stress tolerance (due to reduced water loss). Vice versa, species with high SLA and low LDMC acquire resources faster, showing high competitive ability but lower stress tolerance (i.e. higher vulnerability to stress).

Thus, we assumed that under the scenario of 1) increasing drought alone (i.e., without temperature limitation), reducing water loss through high LDMC is a relevant strategy (Ackerly, 2004; Grime, 2001; Liancourt *et al.*, 2015); 2) combined increases of drought and temperature, LDMC may increase while SLA decreases (Liancourt *et al.*, 2015); 3) increasing nutrients, a rapid resource-acquisitive strategy (i.e., high SLA) is beneficial and would confer a competitive advantage under the subsequent increase in competition (Garnier *et al.*, 2016; Liancourt *et al.*, 2013; Wright *et al.*, 2005). A scenario with temperature increase alone was not assessed because it is reasonable to assume that in such dry alpine ecosystem temperature increase alone, without changing water availability, would result in a more drought stress (i.e., scenario 1 and 2, IPCC (2014)).

The trait measurement procedure followed a standard protocol (Pérez-Harguindeguy *et al.*, 2013). For each individual subordinate plant and for five individuals of each foundation species the best-developed and most healthy leaf was collected (n = 1340). Leaves were fully rehydrated before determining the fresh mass and the leaf area, then they were dried at 80°C for at least 72 h to determine dry mass. SLA was measured as the ratio between leaf area measured as one-sided surface area of an individual lamina (m^2) and leaf dry mass (m^2 kg^{-1}), and LDMC was measured as the ratio between leaf dry mass and water-saturated fresh mass (g kg^{-1}). The sampling took place at the peak of the growing season, between the end of July and the beginning of August 2011.

Plant association network

The network was built from the observed community matrix, i.e. The set of abundance data for n subordinate species growing within m microhabitats (i.e., the three foundation species and open areas), considering all plant species as nodes and co-occurrence between subordinate species and foundation species or open areas as pairwise links (Figure 6).

Then, the one preferred microhabitat for each subordinate species was identified with a community structure detection algorithm, which computed optimal partitioning of species into the four microhabitats. This algorithm maximizes modularity with simulated annealing according to patterns of intra- and inter-module connections (Doulcier & Stouffer, 2015; Guimera & Nunes Amaral, 2005).

Species extinction model

The species extinction procedure as a consequence of simulated environmental changes consisted of three main steps. First, for each iteration of primary extinction (see below), a species trait value was sampled from its trait distribution (i.e., a normal distribution with a mean equal to each species' observed trait mean over all microhabitats and the standard deviation equal to each species' observed standard deviation). With this procedure we accounted for intraspecific

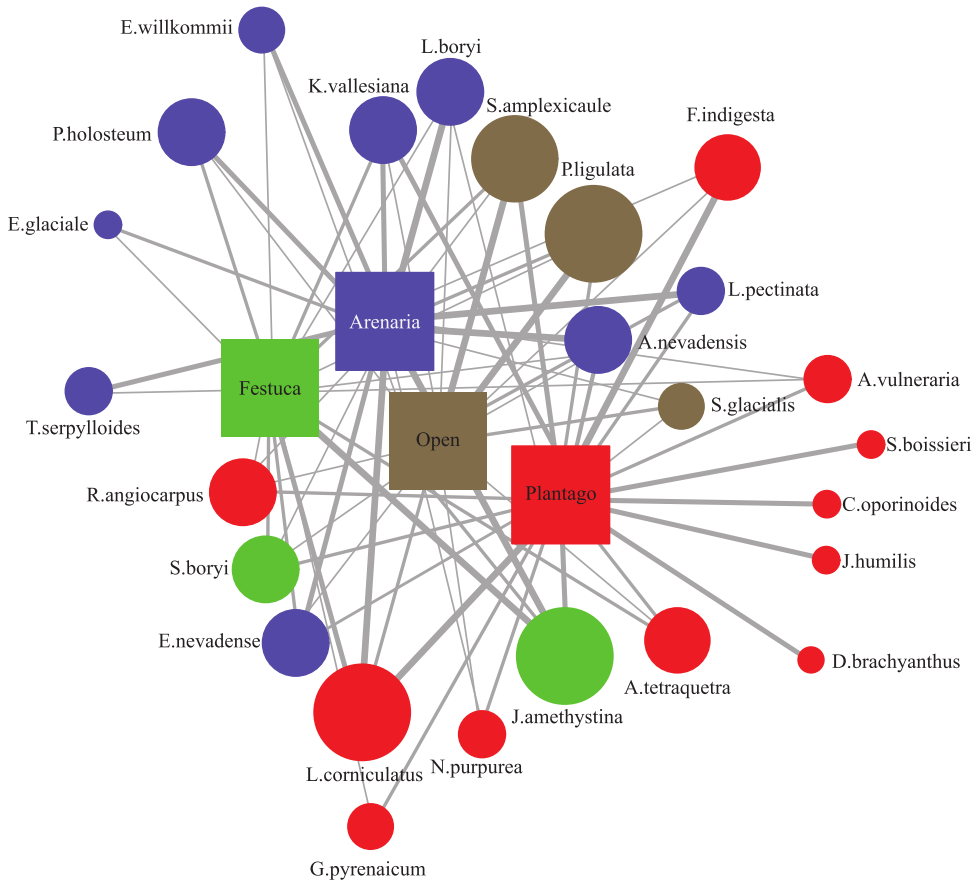

Figure 6 Plant–plant network in the Sierra Nevada, Spain. Plant species are represented by nodes, whose dimensions are proportional to the species abundance. Links are proportional to the number of links (i.e., individuals) between species. Link length depends on node position according to the Kamada & Kawai force-directed algorithm (Csárdi & Nepusz, 2006). Microhabitats are represented by rectangles, subordinate species by circles. Colours depict network modules (i.e., microhabitat preferences): blue for *Arenaria tetraquetra* spp. *amabilis*, green for *Festuca indigesta*, red for *Plantago holosteum*, and brown for open microhabitat.

trait variation at the study site (i.e., species trait plasticity, Fig. S2).

Second, based on the above-mentioned relationships among leaf traits and environmental conditions, species were removed according to the following criteria. For increasing drought alone (hereafter scenario D), species were removed in order of increasing LDMC, with species having the lowest LDMC to be removed first. As increase in drought and temperature (hereafter scenario D & T) is based on both LDMC and SLA, in order to sort plant species within this bivariate trait space, a principal component analysis (PCA) was carried out, including species trait values as active variables. First, the correlation coefficients between the two variables were evaluated. Since we expected an inverse relationship between LDMC and SLA (Pérez-Harguindeguy *et al.*, 2013), we selected the main axis of the PCA that described the negative correlation between these two traits. Then, species were sorted according to their coordinates on the axis and removed in order of increasing values, with species having the lowest values along the selected axis (i.e. Low LDMC and high SLA) to be removed first. For increasing nitrogen deposition (hereafter scenario N), species were removed in order of increasing SLA, with species having the lowest SLA to be removed first. Besides these three environmental change scenarios, we performed a random extinction model (hereafter scenario R) by randomly

removing species from the network. For each scenario the corresponding trait space was divided into 25 equally spaced intervals, representing the primary extinction sequence. At each step (1, 2, 3, ..., 25), an increasing number of intervals of the trait range was removed from the viable trait space and plant species that did not fit this viable trait space were removed from the network. In other words, plant species that fell out of the range of surviving trait values were considered primary extinct. In the scenario R, an equal number of species was removed in each extinction sequence.

Therefore, different to previous extinction models (Dunne *et al.*, 2002; Memmott *et al.*, 2004; Solé & Montoya, 2001; Verdú & Valiente-Banuet, 2008), such as scenario R, the biology-informed extinction sequences using functional traits could result in unequal numbers of species removed from the network during each primary extinction iteration, depending exclusively on the number of species assigned to each trait interval.

Third, besides primary extinctions, we considered also secondary extinctions (*sensu* Brodie *et al.* (2014). Since each foundation species provides specific and unique microenvironmental conditions (Butterfield & Callaway, 2013; Ellison *et al.*, 2005; McIntire & Fajardo, 2014; Schöb *et al.*, 2013a, 2012), their loss can be compared to the loss of a microhabitat. Thus, we defined secondary extinctions as the loss of subordinate species due to microhabitat loss, i.e. The loss of those species that belonged to the module of a foundation species that got primary extinct.

Every primary extinction step was iterated 200 times (n replicates= 25'000). At the end of each iteration we computed: a) the proportion of surviving species (i.e., relative species richness) within the network, calculated as the sum of species that survived divided by the total species richness; b) the proportion of secondary extinctions, calculated as the sum of secondary extinctions divided by the total number of extinctions (i.e., primary plus secondary); c) the persistence status of each plant species (i.e., survival, primary or secondary extinct).

Statistical analysis

We used linear mixed effects models to test the response variables (1) proportion of surviving species and (2) proportion of secondary extinctions as a function of the extinction scenarios (fixed effect), number of foundations species (fixed effect), and their interaction (fixed effect), with random effects being the iteration nested within each extinction step. To account for series autocorrelation, the steps along the sequences within each scenario were included in the first order correlation model for the residual error component (Butler *et al.*, 2007). The significance of the models was tested with Wald tests.

To confirm the relevance of the model, we assessed whether subordinate species differed in their probability of surviving or getting secondary extinct by fitting a multinomial logit model with the status of the species (survived, primary or secondary extinct) as response categories and the species as predictors (Venables & Ripley, 2002). The primary extinction was considered as reference level.

Then, in order to explore which biotic factors make species more likely to persist or to get secondary extinct, generalised linear models (GLM) were fitted with the module membership

Table 1 Fixed effects test and variance component estimates (standard error) for linear mixed-effects models. The number of foundation species and its interaction with the five environmental change scenarios are predictors of species survival and secondary extinctions. $***$ $p < 0.001$.

	Species survival	**Secondary extinctions**
Fixed effects		
Intercept	$F_{1,13'163} = 70.0 * **$	$F_{1,15'015} = 10.4 * **$
scenario	$F_{3,13'163} = 838.6 * **$	$F_{3,15'015} = 3230 * **$
foundation sp	$F_{3,13'163} = 12310 * **$	$F_{3,15'015} = 14080 * **$
scenario x Found.	$F_{9,13'163} = 345.4 * **$	$F_{9,15'015} = 136.2 * **$
random effects		
Step/Iteration	$9 \times 10^{-3}(1.0 \times 10^{-5})$	$5.3 \times 10^{-7}(3.4 \times 10^{-11})$
Series autocor		
ρ AR(1)	$0.5(6.1 \times 10^{-3})$	$0.4(6.6 \times 10^{-3})$

and the abundance of each subordinate species as predictors and the likelihood (i.e. the logit estimated by the multinomial logit model) of survival or to get secondary extinct as responses. The likelihood to get primary extinct was taken as reference level for these analyses. The significance of the models was tested with ANOVA tests and likelihood-ratio χ^2 estimation.

Analyses were performed in R 3.1.3. (R Core Team, 2017) using *igraph* for network analysis (Csárdi & Nepusz, 2006), *Rnetcarto* for network modularity (Doulcier & Stouffer, 2015), *asreml* for mixed effects models (Butler *et al.*, 2007), *pascal* for Wald tests and *nnet* for the multinomial logit model (Venables & Ripley, 2002).

Results

Plant association network response

The plant association network was composed of four modules corresponding to the four micro-habitat types (Figure 6). The *Plantago* module was the most species rich, with 11 associated subordinate species, followed by the *Arenaria* module composed of 9 associated subordinate species, the *Festuca* module with 2 associated subordinate species, and the open module with 3 associated subordinate species.

The three environmental change scenarios and the number of foundation species had significantly interactive effects on the proportion of surviving species (Table 1).

In scenario D of increasing drought alone, in scenario D & T of increasing drought and temperature, and in scenario random, species diversity smoothly decreased in the first half of the sequence, with, on average, 50% of the species disappearing after removal of c. 40% of the trait space (Figure 7).Then, in the second half of the sequence a further intensification of environmental changes caused less extinction.

In scenario D, *Arenaria*, *Plantago*, and *Festuca* disappeared after removal of 39%, 23%, and 48% of the trait space, respectively, while in scenario D & T they disappeared after 23%, 26%, and 34%, respectively. These scenarios produced less secondary extinction events (4% and 5% on average, respectively) and created hump-shaped responses of secondary extinctions, which

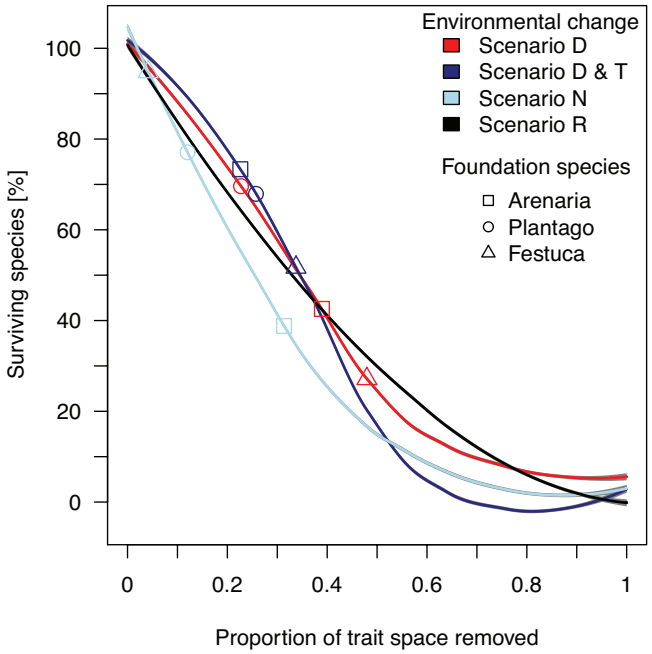

Figure 7 Species diversity response (y-axis) to the three environmental change scenarios and the random model along the removal sequence (x-axis). Scenario D: increasing drought alone; scenario D & T: increasing drought and temperature; scenario N: increasing nitrogen deposition; scenario R: random model. Squares (*Arenaria tetraquetra* ssp. *amabilis*), circles (*Plantago holosteum*) and triangles (*Festuca indigesta*) show where each foundation species goes extinct on average. Lines fitted with a local polynomial surface (mean ± 95% CI).

made up to 10% of the species losses when 56% and 49% of the trait spaces were removed, respectively (Figure 8).

In scenario N of increasing nitrogen deposition produced a constant steep decline in species diversity, with 50% of species disappearing when *c.* 25% of the trait space was removed (Fig. 2). After removal of 40% of the trait space, species diversity showed a slower non-linear decrease. This scenario caused the highest secondary extinction rates (on average 20%), with a right-skewed hump-shaped pattern along the trait range removal sequence (Figure 8). Here, *Arenaria*, *Plantago*, and *Festuca* disappeared after removal of 31%, 12% and 4% of the trait space, respectively.

Subordinate species persistence

Subordinate plant species exhibited different likelihood of survival or secondary extinction within the network. (Figure 9, Tab. S1). Over all scenarios, module membership significantly explained the likelihood of subordinate species to survive or get secondary extinct ($G^2_3 = 23.17$, $p < 0.001$, $G^2_3 = 581.98$, $p < 0.001$, respectively; Tab. S2).

Subordinate species associated to *Arenaria* and *Plantago* modules were significantly less likely to survive ($t = -2.58$, $p < 0.05$, $t = -2.87$, $P < 0.05$, respectively), and significantly more likely to get secondary extinct ($t = 12.89$, $p < 0.001$, $t = 15.21$, $p < 0.001$, respectively) compared to subordinate species associated with *Festuca* and the open microhabitat.

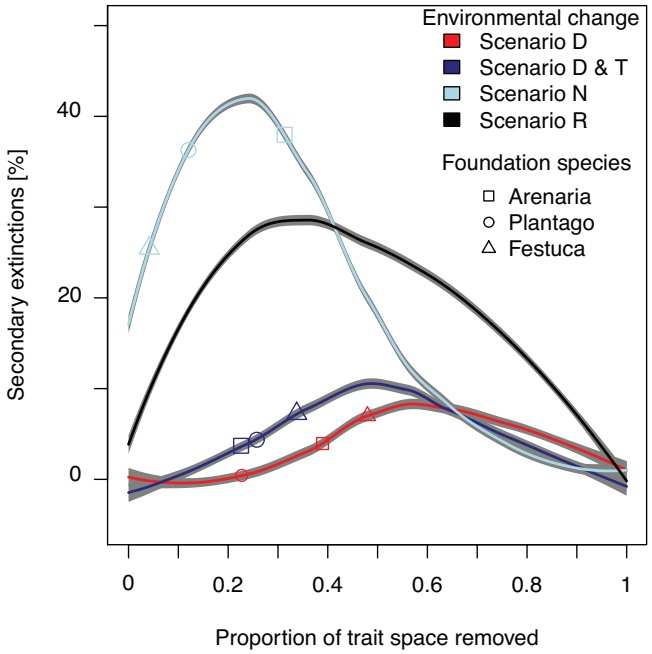

Figure 8 Secondary extinctions (y-axis) in response to the three environmental change scenarios and the random model along the removal sequence (x-axis). Scenario D: increasing drought alone; scenario D & T: increasing drought and temperature; scenario N: increasing nitrogen deposition; scenario R: random model. Squares (*Arenaria tetraquetra* ssp. *amabilis*), circles (*Plantago holosteum*) and triangles (*Festuca indigesta*) show where each foundation species goes extinct on average. Lines fitted with a local polynomial surface (mean ± 95% CI).

Discussion

Our assessment of the resistance of alpine plant communities to microhabitat loss using functional traits as a proxy for species' susceptibility showed that extinction rates were dependent on the type of environmental perturbation. Indeed, the order and timing of breakdown of the plant interaction network sustained by the foundation species differed substantially among the three environmental change drivers.The plant interaction network underlying the studied plant community was rather fragile to a simulated increase in nitrogen deposition. Conversely, the plant interaction network resisted against moderate drought alone or drought combined with temperature increases. Community persistence against these latter environmental perturbations can be explained by the fact that in these two scenarios foundation species remained longer in the network, thereby slowing down biodiversity loss compared to a random extinction simulation.

These results might indicate the relevance of plant association networks in modulating the impact of different environmental changes on species diversity and community persistence. Thus, within the limits of our assumptions, predictions of the fate of species and communities depend on the knowledge of the main driver of environmental change at the location of interest and how this environmental perturbation affects the plant interaction network.

Climate warming has recently been proved to change the composition and the structure of alpine plant communities, leading to a decline and disappearance of cold-adapted plant species (Gottfried *et al.*, 2012). Furthermore, Hautier *et al.* (2015) found a biodiversity decline

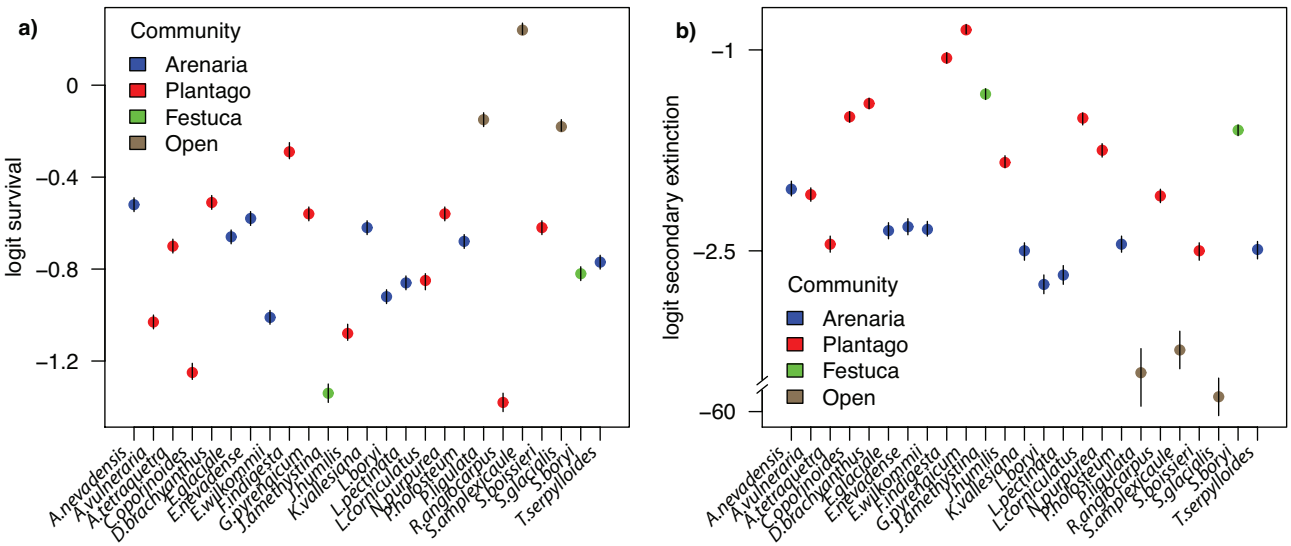

Figure 9 Multinomial log-linear model of the differences among subordinate species (x-axis) in their probability (i.e., logit) of persistence within the network (y-axis), i.e., surviving **(a)** or getting secondary extinct **(b)**. For the 95% confidence intervals (y-axis in **(b)** rescaled for clarity), see Tab. S1.

in response to nitrogen enrichment in experimental grassland communities. Our simulation suggested that nitrogen deposition could alter plant network structure, resulting in potentially accelerated species loss.

In other words, just a small shift in the corresponding functional trait space, i.e., a removal of species with lower SLA values, caused the loss of foundation species and therefore a disproportionate increase in secondary extinctions. This is consistent with a fragile ecosystem in which small environmental perturbation causes the primary extinction of a small but important fraction of species that have critical cascading effects (Fortuna & Bascompte, 2006; Memmott *et al.*, 2007; Rezende *et al.*, 2007).

Species distribution models suggest that decreasing precipitation plays an important role in determining the potential impacts of climate change on vegetation, mainly due to habitat loss (Engler *et al.*, 2011). We found that drought may not be the main driving factor for species loss in the dry alpine climate of the Sierra Nevada (Spain). We suggest that the general tolerance to drought of the species growing in this environment (Giménez-Benavides *et al.*, 2007), in particular that of foundation species, might actually allow this vegetation to better resist further increase in drought compared to other environmental perturbations.

Having shown that plant–plant interaction networks responded in different ways to different environmental perturbations, we next explored how the role of foundation species differed across the different scenarios. The emerging patterns of secondary extinctions with increasing drought alone or increasing drought combined with temperature probably resemble the pattern of extinctions following the order in species abundance, with rare species becoming extinct first (Memmott *et al.*, 2004).

Under these circumstances, it is expected that the loss of least connected (Dunne *et al.*, 2002; Solé & Montoya, 2001) or least abundant (Verdú & Valiente-Banuet, 2008) species does not have important negative consequences on network structure. Conversely, in the scenarios

N, where foundation species got lost early in the extinction sequence, species diversity declined rapidly also due to higher rates of secondary extinctions.

This suggests that in our study system, increases in nitrogen availability might negatively affect survival of the foundation species. This might be due to increasing competitive pressure from colonizing subordinate species (Schöb *et al.*, 2013b, 2014b), and finally competitive exclusion of the foundation species (McAuliffe, 1984).

Taken together, in this dry alpine ecosystem dominated by drought-tolerant species, moderate increases in drought stress may not have important consequences for the plant community (Miranda *et al.*, 2009). This effect might particularly be due to the high drought resistance of the foundation species present (Schöb *et al.*, 2013a, 2012) and the role these species play in the plant interaction network. On the other hand, changes that favour more competitive species might accelerate changes in the plant community (Michalet *et al.*, 2014), also due to the extinction of the less competitive foundation species (Liancourt *et al.*, 2005; Maestre *et al.*, 2009; McAuliffe, 1984).

Conclusions

Our study is one of the few attempts to analyse the consequences of environmental changes on ecological networks and their species by taking into account the species' sensitivities to those environmental drivers (Tylianakis *et al.*, 2008). Our simulation approach approximates species deletion according to global trait-environment relationships. Furthermore, we take into account that species are plastic and include the observed trait plasticity in our models. Thus, our trait-based extinction model in response to environmental changes is biology-informed, and therefore likely to be more ecologically meaningful than previous extinction models based only on the level of species interconnectedness (i.e., species degree) or random species removal (e.g. Dunne *et al.*, 2002; Memmott *et al.*, 2004; Solé & Montoya, 2001; Verdú & Valiente-Banuet, 2008). Nevertheless, our study has limitations in that it is mainly static: we did not account for birth and mortality changes within species, nor for range shifts of species into new potentially suitable habitats, nor the immigration of new species from lower altitudes. We did not consider potential changes in network structure nor the interaction rewiring, i.e., the establishment of new interactions. Furthermore, we ignored the potential effects of differences in microhabitat size. Nevertheless, our approach represents a conceptual advance for linking functional ecology with network theory into a unified framework that could improve predictions of community responses to environmental change. As such, we foster its use with all types of interactions (e.g. predator–prey), environmental changes (e.g. disturbance) and corresponding response traits (e.g. body mass).

Acknowledgements

This study was financially supported by the Swiss National Science foundation (PZ00P3_148261). We thank N. Pistón, P. Macek and F.I. Pugnaire for their help with data collection. We thank

J. Bascompte, R. Michalet, M.A. Fortuna, M. Caccianiga and G.M. Palamara for their fruitful discussions, and B. Schmid for helping with mixed-effects models. In addition, we wish to thank the Associate Editor, Mikey O'Brien and Takehiro Sasaki for commenting on an earlier version of this manuscript. Authors disclose any potential sources of conflict of interest.

Data Accessibility

Network data available from the Dryad Digital Repository
`http://dx.doi.org/10.5061/dryad.35q01`

Supporting Information

Conceptual framework, trait distributions and model coefficients.
`R script` uploaded as supporting information.
`http://onlinelibrary.wiley.com/doi/10.1111/1365-2435.12839/full`

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No 29, Spring 2016

Upcoming Events

Fachtagung – Neue Technologien im Pflanzenschutz
8 Jun 2016, ETH Zurich

PLANT FELLOWS Symposium – Final Meeting
23 Jun 2016, Zurich

PSC Summer School – Agriculture in Transformation
11-16 and 19 Sep 2016, Einsiedeln

Cover picture of number 29 of Plant Science Center (PSC) Newsletter, Spring 2016.
Sampling of cushion plant community within 20 x 20 cm plots in the high-elevation Sierra Nevada Mountains in Spain. The foundation species *Arenaria tetraquetra* spp. *amabilis* and the beneficiary species *Jasione amethystina*, *Sideritis glacialis* and *Anthyllis vulneraria* spp. *pseudoarundana* growing upon its cushion. In this harsh environment, foundation species provide facilitative effects for growing and survival of subordinate beneficiary species.

Chapter three

Facilitation between plants shapes pollination networks.

Communities are not produced by summing the population ecology of species.
— Ragan M. Callaway

This chapter is based on the manuscript: Losapio, G., Fortuna, M.A., Bascompte, J., Schmid, B., Michalet, R., Neumeyer, R., Castro, L., Cerretti, P., Germann, C., Haenni, J-P., Klopfstein, S., Ortiz, J., Pont, A.C., Rousse, P., Schmid, J., Sommaggio, D. & Schöb, C. 2017b. Facilitation between plants shapes pollination networks. *bioRxiv*, 161034. https://doi.org/10.1101/161034.

Significance

Despite the fundamental importance of plant–plant interactions for biodiversity and ecosystem functioning, the details of how competition and facilitation among plants scale up to mutualistic interactions with pollinators and their networks are poorly understood. We introduce a simple experimental system in which we control local plant interactions, measure pollinator responses and characterise plant–plant facilitation effects on plant–pollinator networks. We find that facilitation among plants produces synergistic and antagonistic effects on the pollinator community affecting the architecture and robustness of pollination networks. Our results provide evidence for the bottom-up non-additive effects of positive plant interactions on pollination networks and have implications for the way we study and manage ecosystems.

Introduction

Plants cluster together and interact among themselves and with other mutualists, with fundamental consequences for biodiversity and ecological networks. However, linkages between interacting plants and plants interacting with mutualists are poorly understood in real-world ecosystems. Here, we report results of a field removal experiment with natural plant communities where we compared networks of pollinators interacting with foundation species and their associated beneficiary species growing in clusters, with networks of pollinators interacting with the same foundation and beneficiary species growing alone. We tested the hypothesis that the network of foundation and beneficiary species growing in multispecific clusters is more nested and robust than the sum of networks of the foundation species and beneficiary species growing separately. We found that pollinator diversity and network architecture was significantly different when foundation and beneficiary species grew together than what would be expected from additive effects of foundation species and beneficiary species. The directionality of these effects varied between foundation species. Moreover, the resulting changes in network-level interaction diversity, independent from species diversity, affected simulated network robustness, with differences among extinction scenarios and foundation species. This study, therefore, sheds new light on the mechanisms behind the propagation of ecological interactions within trophic levels to interactions among trophic levels in real-world networks and suggests that non-additive effects should emerge in a variety of interactions and systems.

Despite wide-ranging implications for biodiversity (Callaway, 2007; Valiente-Banuet *et al.*, 2006), ecosystem functioning (Hector *et al.*, 1999) and services (Duchene *et al.*, 2017; Schöb *et al.*, 2015), fundamental questions remain about the basic ecological role plant–plant interactions play in real-world ecosystems (McIntire & Fajardo, 2014). Interactions among plant species can be positive (i.e., facilitation), neutral, or negative (i.e., competition) depending on whether the presence of plants enhances or diminishes the growth, survival, or reproduction of

neighbours, respectively (Callaway, 2007). Independently of the underlying mechanisms, facilitation and competition mainly result in spatial aggregation (i.e., clustering) and segregation (i.e., exclusion), respectively (Bruno *et al.*, 2003; MacArthur & Levins, 1967; Meron, 2012). Facilitation is often due to the effect of foundation species, i.e., species tolerant to stress that buffer limiting environmental factors in a way that some other, associated species can benefit from the newly created environmental conditions (Bruno *et al.*, 2003; Callaway, 2007; Ellison *et al.*, 2005; McIntire & Fajardo, 2014). Generally, facilitation is now recognised as a fundamental ecological process in plant communities (Callaway, 2007) and ecosystems (Duchene *et al.*, 2017). Particularly, foundation species can structure plant communities (Schöb *et al.*, 2012) by enabling species coexistence (McIntire & Fajardo, 2014) and increasing plant diversity (Cavieres *et al.*, 2014; Hacker & Gaines, 1997; Michalet *et al.*, 2006).

A small number of previous studies has investigated the impact of interactions among plants on pollinators (Carvalheiro *et al.*, 2014; Feldman *et al.*, 2004; Mesgaran *et al.*, 2017; Molina-Montenegro *et al.*, 2008; Ruttan *et al.*, 2016; Sieber *et al.*, 2011), highlighting the linkages between the structure of plant and insect communities. However, no research has experimentally examined how facilitative plant–plant interactions may propagate to other trophic levels and shapes e.g. pollination network architecture.

Interestingly, the growing interest for positive plant interactions coincided with the growing evidence about the important role ecological networks of mutualistic interactions play in biodiversity maintenance (Bascompte & Jordano, 2014; Bastolla *et al.*, 2009). Indeed, simultaneously but independently, the study of mutualistic networks among plants and animals has illustrated ecological and evolutionary processes shaping communities and ecosystems (Bascompte & Jordano, 2014).

Differences between those two fields reside in that plant ecology has hardly considered interaction networks within plant communities (Losapio & Schöb, 2017) while ecological networks mainly focused on interactions between trophic levels (but see e.g. Verdú & Valiente-Banuet (2008)). Consequently, there is a lack of studies experimentally investigating how interactions among plants scale up to mutualistic networks in real-world ecosystems. In particular, we do not know to what extent plant facilitation has bottom-up cascading effects shaping the architecture and robustness of plant–pollinator networks.

To this end, we conducted a field removal experiment with two foundation species (*sensu* Ellison *et al.*, 2005) (*Arenaria tetraquetra* spp. *amabilis*, hereafter *Arenaria* and *Hormathophylla spinosa*, hereafter *Hormathophylla*) and eight beneficiary species (Fig. SI1) in the Sierra Nevada Mountains (Spain), where the importance of plant facilitation for community structure is well documented (Schöb *et al.*, 2013a,b, 2012, 2014b).

We assembled plant communities with foundation species and beneficiary species growing together in clusters (i.e., resembling the facilitation effect) and the same foundation species and beneficiary species growing separately (i.e., resembling the two different parts of the facilitative system in isolation) and we recorded plant–pollinator interactions. To experimentally test the hypothesis that pollination networks of facilitation-driven plant clusters are more diverse,

nested, and robust than what would be expected from summing pollination networks of foundation and beneficiary species growing separately (Figure 10) we compared the observed pollination networks of foundation and beneficiary species growing together (i.e., the 'facilitation' treatment) with the expected pollination networks calculated as the sum of foundation and beneficiary species growing separately (hereafter referred to as 'additive' treatment). Finally, to disentangle the effect of interaction rewiring, i.e., the establishment of new interactions, from species turnover on differences in the expected additive network from the observed facilitation network we considered the pollination networks composed only by species common to both treatments.

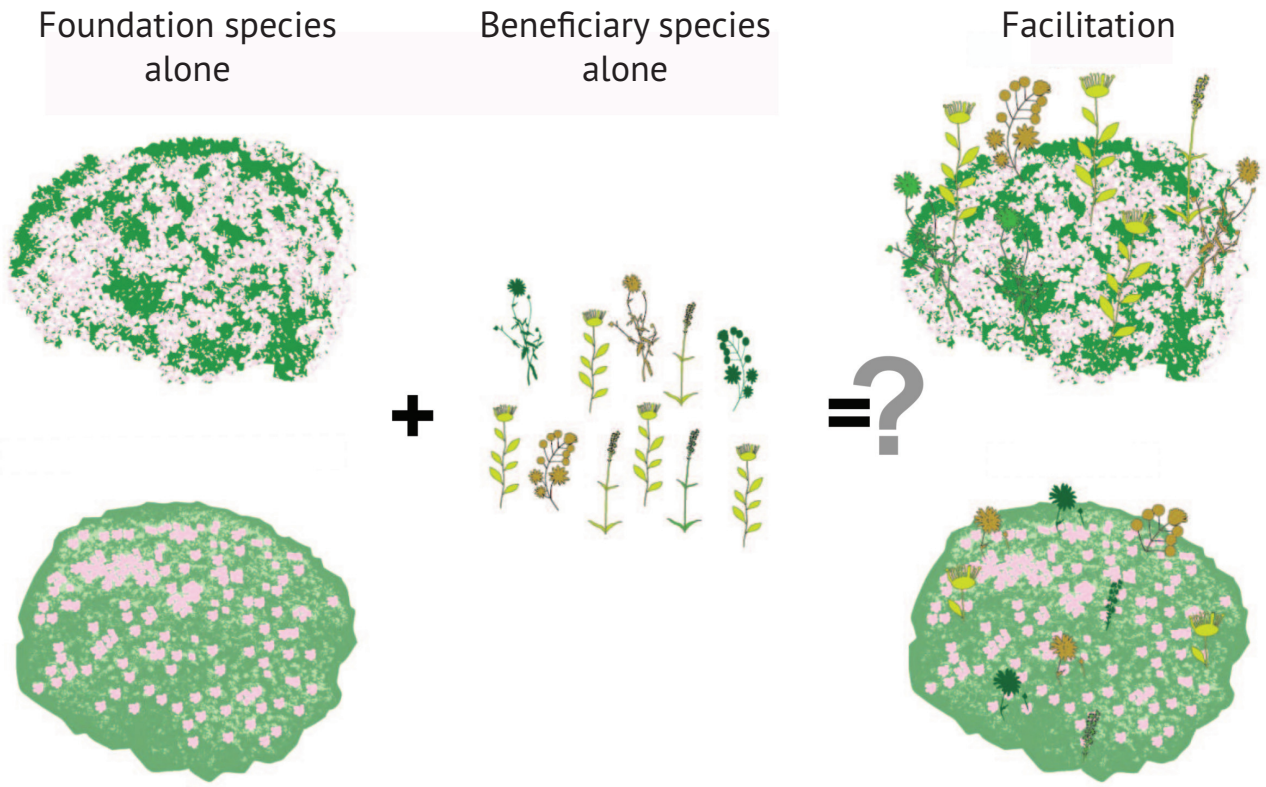


Figure 10 Overview of the experimental design to assess non-additive effects among plant species on pollinator networks. 'foundation species alone': a cushion of the foundation species *Arenaria tetraquetra* spp. *amabilis* or *Hormathophylla spinosa* growing alone; 'Beneficiary species alone': non-cushion plant species growing alone; 'facilitation': *Arenaria* or *Hormathophylla* and associated beneficiary species growing together.

Results

Pollinator diversity

We found that pollinator diversity significantly differed between the observed facilitation clusters and the expected additive sum depending on the identity of foundation species ($F_{1,52} = 5.96$, $p = 0.0017$, Figure 11, Tab. SI1). In particular, the facilitation clusters of *Arenaria* attracted a pollinator community that was c. 60% more diverse than the additive expectation given by the simple sum of foundation and beneficiary species growing separately (q= 0.59, $p = 0.0187$). Differences were not significant for *Hormathophylla* (q= −0.32, $p = 0.3600$). Interestingly, these

results suggest that in the case of facilitation by *Arenaria* net effects on pollinator diversity are synergistic rather than additive.

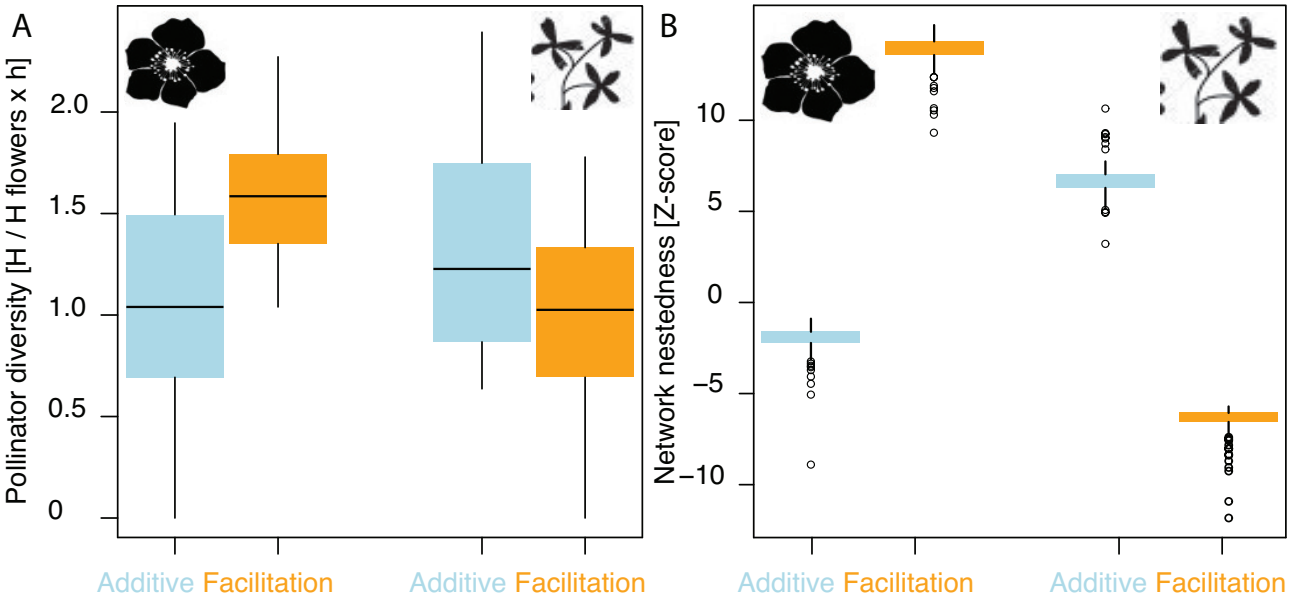


Figure 11 Differences between the expected additive community and the observed facilitation clusters in pollinator diversity and network architecture. (A) pollinator Shannon diversity in expected networks assuming additive effects (light blue) and in observed facilitation networks (orange) of *Arenaria* (left) and *Hormathophylla* (right). Expected additive networks were obtained by summing the networks of foundation species alone and beneficiary species alone. (B) Nestedness of plant–pollinator networks. To compare nestedness among networks of different size, we calculated the relative nestedness (i.e., the Z-score, see Methods). In the box plots, horizontal bars show the median, the box the interquartile range and the vertical lines ± 3 sd.

Visitation rate

For each plant species we assessed the potential beneficial effects of growing in facilitation clusters for pollinator attractiveness (Fig. SI2). The pollinator visitation rate differed between treatments depending on the foundation species ($F_{1,176} = 4.24$, $p = 0.0409$) with average positive and negative effects in *Arenaria* and *Hormathophylla*, respectively (Fig. SI2, Tab. SI1). This indicates that chances of getting visited by pollinators varied when plant species grew in facilitation clusters or not, with contrasting consequences depending on foundation species. For instance, for *Jasione amethystina* and *Lotus corniculatus* subsp *glacialis* pollinator visitation rate increased and decreased under facilitation conditions in *Arenaria* and *Hormathoyphylla*, respectively.

Network architecture

To analyse architectural changes between observed facilitation networks and expected additive networks we compared the relative nestedness (Figure 11). Relative nestedness significantly changed between facilitation and additive networks ($F_{1,396} = 175.85$, $p < 0.0001$) with differences between the two foundation species (interaction term: $F_{1,396} = 21179.7$, $p < 0.0001$, Tab. SI1). Specifically, *Arenaria* facilitation clusters showed a 16-fold increase in network nestedness in comparison with what would be expected assuming additive effects (q= 15.88, $p < 0.0001$).

In contrast, *Hormathophylla* facilitation clusters were 13-fold less nested than the expected additive networks (q= −13.23, $p < 0.0001$). Taken together, these results demonstrate that observed facilitation clusters show also non-additive effects on pollination network architecture in contrasting ways depending on foundation species identity.

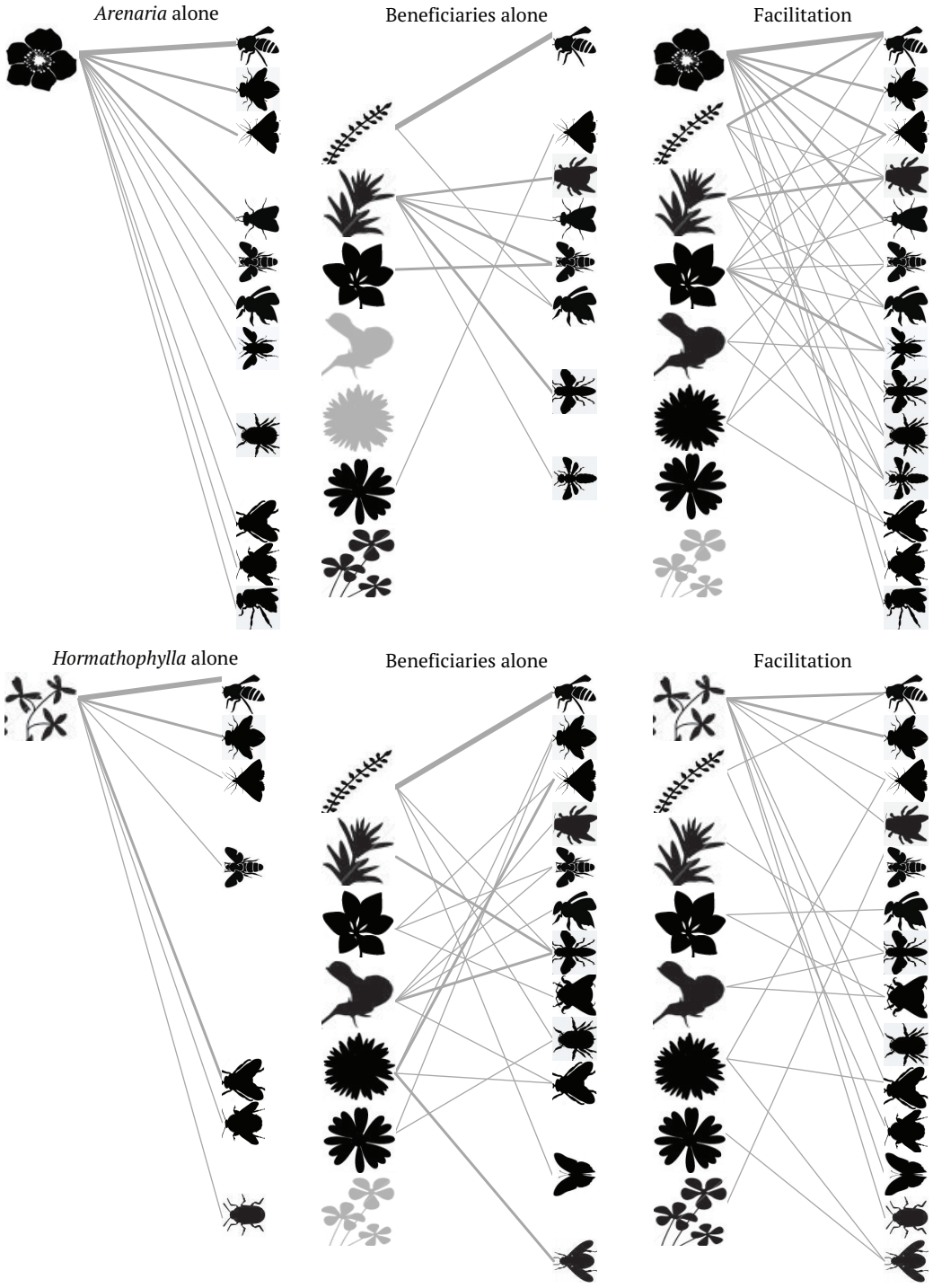


Figure 12 Plant–pollinator networks in experimental treatments composed only by pollinators common to observed facilitation networks and expected additive networks (i.e., the sum of foundation species alone and benefciaries alone). The width of the links is proportional to interaction strength, measured as number of pollinators visiting a flower during one hour. Plants in black and without links were visited only in the network consisting of the entire pollinator species pool. Plants in grey were present but were not visited. For species names, see Fig. SI1. A visual inspection highlights the higher complexity of facilitation networks in *Arenaria* (above) and the lack thereof in *Hormathophylla* (below) compared to the expected sum of 'alone' networks.

Species turnover and interaction rewiring

In order to examine the potential mechanisms that might explain non-additive effects and their consequences for network robustness, we disentangled differences due to changes in species composition from differences due to interaction rewiring, i.e., the changes in interactions between plants and pollinators present in both additive and facilitation networks. Hence, we first quantified the network dissimilarity between expected and observed networks using the beta diversity of interactions (Poisot *et al.*, 2012). network dissimilarity equals to 42.3% for both foundation species (Fig. SI3). In *Arenaria*, 20.0% of this difference is due to interaction rewiring and 22.3% is due to species turnover. In *Hormathohylla*, 25.0% of this is due to interaction rewiring and 17.3% is due to species turnover. These results indicate that networks are different between treatments because they have both different species and because the species they share show different interactions.

Interaction diversity

Having shown that changes in interactions contribute to differences between networks, we proceeded with examining networks composed only by common species to both additive and facilitation networks (Figure 12) in order to exclude differences due to species richness and composition . We found that species-level interaction diversity significantly differed between treatments and foundation species ($F_{1,57} = 10.94$, $p = 0.0016$, Figure 4A, Tab. SI1). Specifically, interaction diversity was higher in *Arenaria* clusters than expected by additive effects (q= 0.48, $p = 0.0044$) but as expected in *Hormathophylla* clusters (q= -0.17, $p = 0.6144$, Tab. SI2). These results indicate that plant facilitation increases the diversity of plant–pollinator interactions in the case of *Arenaria*, while the general effect was neutral in *Hormathophylla*. This interaction plasticity went along with a general increase in the generalisation level of interactions within *Arenaria* clusters.

Network robustness

Network robustness against species loss differed between treatments and foundation species with net effects varying depending on extinction scenarios ($F_{2,792} = 33.67$, $p < 0.0001$, Figure 13 B,C). In five cases out of six, the bottom-up effects of plant facilitation on pollination networks resulted in significantly different network robustness than what we would expect from additive effects of foundation and beneficiary species (Tab. SI2). Specifically, in a random scenario the facilitation networks were c. 2 times more robust than expected for *Arenaria* (q= 1.75, $p < 0.0001$) but not for *Hormathophylla* (q= -0.23, $p = 0.3636$). In extinction scenarios that followed the relative abundance of interactions of plant and pollinator species (i.e., specialised scenario), respectively, pollinator and plant communities in *Arenaria* facilitation networks were 90% more (q= 0.91, $p < 0.0001$) and 2 times less (q= -2.02, $p < 0.0001$) robust than additive networks, respectively, while in *Hormathophylla* for both scenarios facilitation networks were significantly less robust (q= -0.70, $p = 0.0001$; q= -1.83, $p < 0.0001$).

In addition, we found that the relationship between interaction diversity and network robustness varied between treatments and foundation species ($F_{1,395} = 57.82$, $p < 0.0001$, Figure 4D; $F_{1,395} = 15.93$, $p < 0.0001$; $F_{1,395} = 59.79$, $p < 0.0001$ for random, specialised plants and specialised pollinators scenarios, respectively). Consequently, the diversity of interactions affected network robustness, regardless of species diversity, in different ways than assuming additive effects. Interestingly, the strength of this relationship varied between networks and foundation species depending on the extinction scenarios (Tab. SI3).

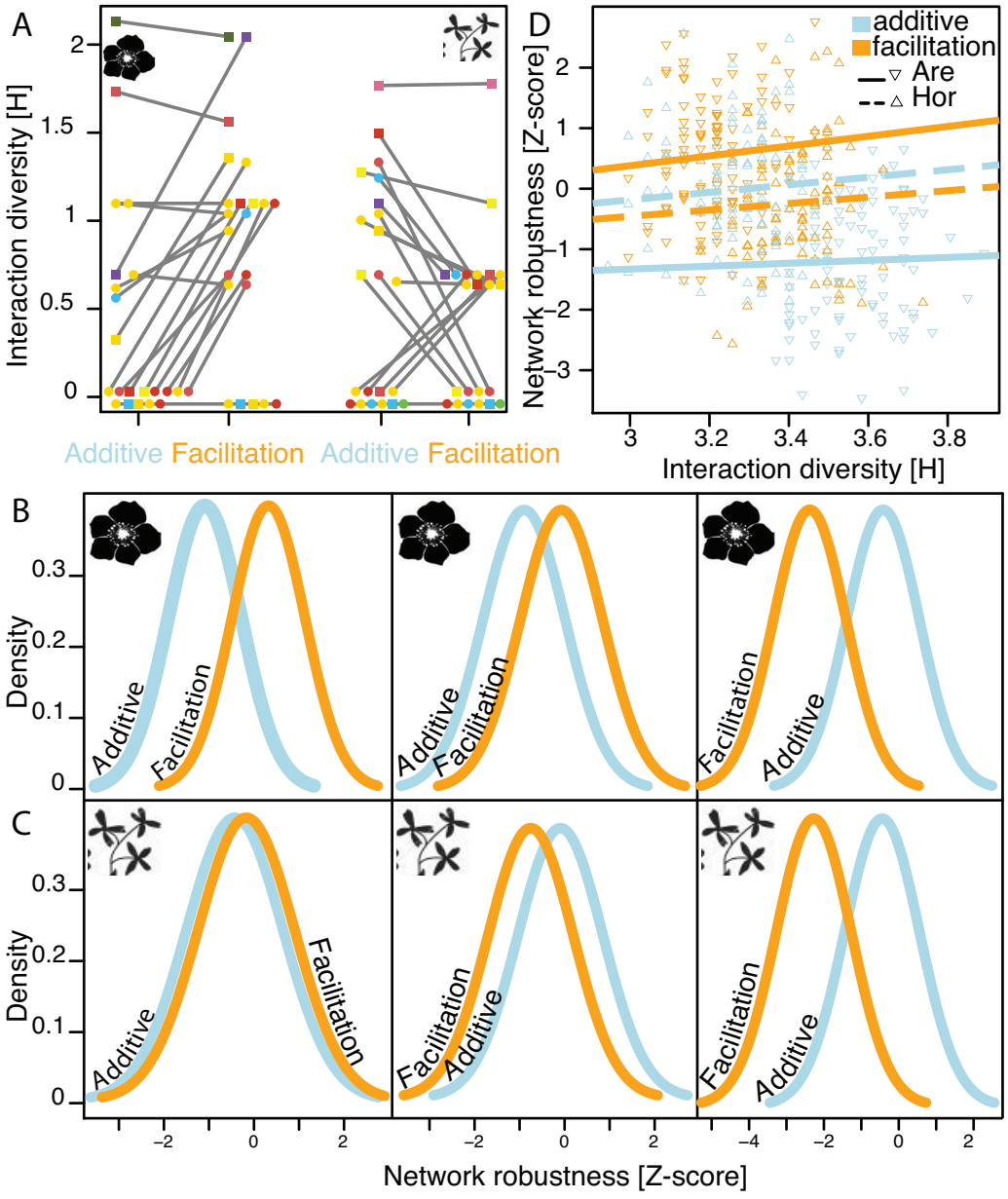


Figure 13 Properties of networks composed of species common between the additive and facilitation networks. (A) interaction diversity of plant and pollinator species in expected additive networks and observed facilitation networks of *Arenaria* (left) and *Hormathophylla* (right). (B,C) Simulated network robustness against species loss (see Methods) of observed facilitation (orange) and expected additive (light blue) networks of *Arenaria* (B) and *Hormathophylla* (C) considering the scenarios of random extinctions (left), specialised-plants extinction (middle, i.e., the pollinator community robustness) and specialised-pollinators extinction (right, i.e., the plant community robustness). (D) The strength of the relationship between network-level interaction diversity and network robustness varies between networks and foundation species, depending on the scenario. Only the case of the random scenario is shown.

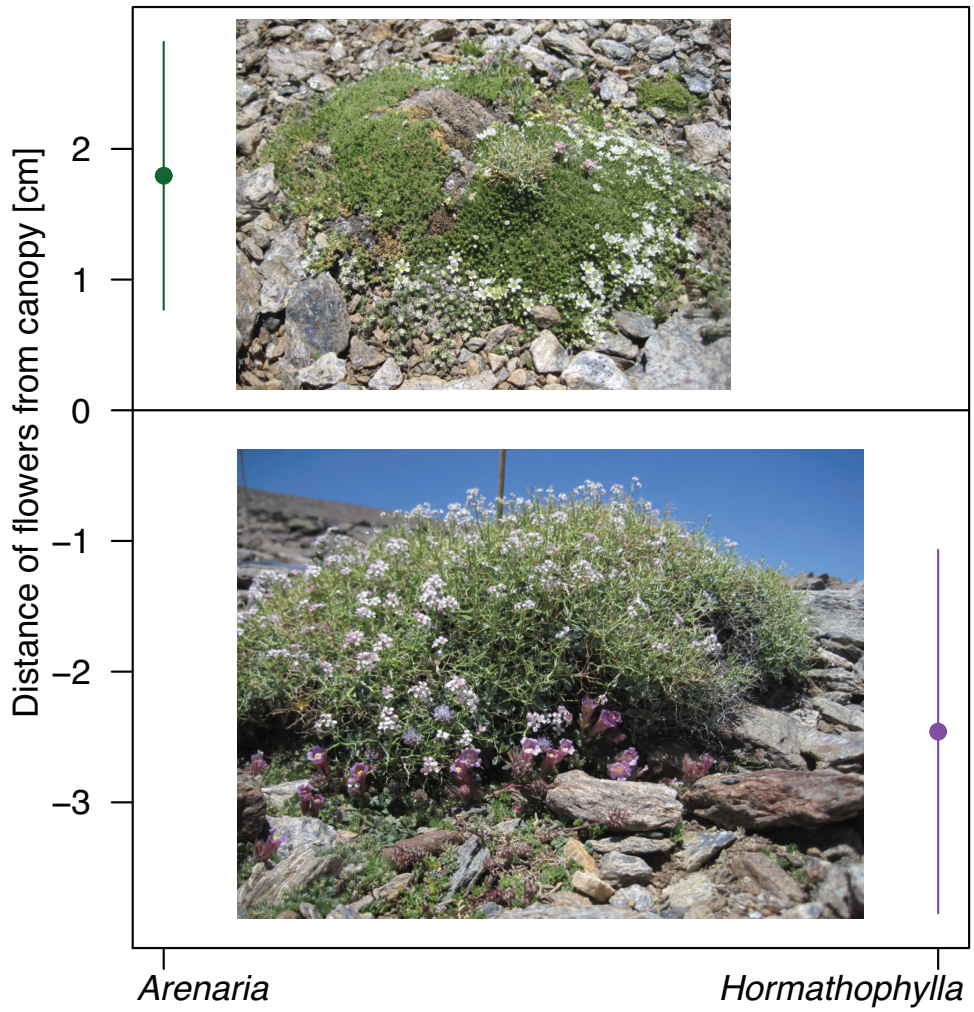


Figure 14 Distance of flowers of beneficiary species from the canopy of *Arenaria* (left and top) and *Hormathophylla* (right and bottom) cushions. Shown are 95% CIs and pictures of the two foundation species with beneficiary species. In compact *Areanaria* cushions, beneficiary species grow on top of it. Conversely, in loose *Hormathphylla* cushions, beneficiary species grow underneath.

The identity of foundation species and the directionality of non-additive effects

We suggest that the differences in the effects of *Arenaria* and *Hormathophylla* on pollinators may be due to the different position of associated beneficiary species within the canopy of the two foundation species ($F_{1,43} = 30.05$, $p < 0.0001$, Figure 14). In *Arenaria*, beneficiary species flower on top of the cushion canopy. Conversely, in *Hormathophylla*, the flowers of beneficiary species rarely reach the canopy and stay beneath. This may result in non-additive effects with a synergistic outcome for *Arenaria* and antagonistic to neutral effects for *Hormathophylla*.

Discussion

We found that plant clustering through facilitation produced non-additive effects that scale up to pollination networks. Observed plant–pollinator interactions were different from expectations based on the sum of foundation and beneficiary species growing separately. This implies that plant–plant facilitation significantly affected plant–pollinator interactions, which in turn affected the architecture and robustness of plant–pollinator networks. The observed plant–

pollinator interactions showed a certain degree of plasticity, that is variability in the identity of interacting partners. The existence of non-additive effects furthermore implies that interactions within a community are different from interactions outside a community context. In our specific case, the directionality of these effects, whether synergistic or antagonistic, depended on the identity of the foundation species, and in the case of robustness also on the extinction scenario.

These findings have implications for broader issues related to the nature of species interactions and the mechanisms regulating biodiversity in natural ecosystems. We argue that reductionist studies of species and their pairwise interactions in isolation from the community context might result in misleading conclusions.

First, our results support the hypothesis that positive plant–plant interactions can influence the assembly of the pollinator community as well as shape plant–pollinator networks. These results are in accordance with other studies showing the beneficial effects of foundation species on insect communities (Molina-Montenegro *et al.*, 2008; Reid & Lortie, 2012; Ruttan *et al.*, 2016). Overall, we found that positive plant interactions can scale up to modify plant–pollinator network architecture and robustness thanks to synergistic effects of plant aggregation and pollinator adaptive responses. Indeed, plant clusters created by facilitation increased the diversity of pollinator species and resulted in more nested plant–pollinator networks in one of two model systems. Furthermore, higher nestedness in the observed facilitation network with *Arenaria* may result in a reduction of competition among plants for pollinators (Bastolla *et al.*, 2009).

Second, we found that the diversity of plant–pollinator interactions affected network robustness regardless of the diversity of species. These results demonstrate that the diversity of species interactions is also relevant for ecosystem stability, an effect often attributed to the diversity of species *per se* (Hooper *et al.*, 2005). High interaction diversity can contribute to network robustness by creating redundancy of links among plants and pollinators. Such redundancy can be achieved on the one hand by higher species diversity, but on the other hand also by increased interaction plasticity of the interacting partners. Indeed, in case of *Arenaria*, we observed not only higher species diversity but also a shift in interaction plasticity, with pollinator interactions in facilitation clusters becoming more generalist than expected. Consequently, facilitation clusters can produce a magnet effect (Laverty, 1992; Molina-Montenegro *et al.*, 2008) that results in increased plant–pollinator interactions.

A third aspect of our results is that the negative effects of plant–plant competition for resources in plant clusters may be counterbalanced by the positive effects of plant–plant facilitation for pollination networks, finally contributing to the overall facilitative effect of foundation species on plant species richness and density (Schöb *et al.*, 2012). On the one hand, the higher density in plant clusters may increase competition among plants for resources (Grace & Tilman, 1990; Harpole & Tilman, 2006; Levine & Rees, 2002). On the other hand, we demonstrate that plant clustering can be beneficial for pollination (see also Feldman *et al.*, 2004; Laverty, 1992; Mesgaran *et al.*, 2017), hence potentially increasing sexual reproduction of plants (Schöb *et al.*,

2014b).

The coexistence of the competing plant species can be explained by the 'cluster effect' (a socio-economical concept *sensu* Porter (Porter, 1998, 2008)) where, in our case, benefits in the pollination service overcome the negative impacts of plant competition. In other words, our study demonstrates that species clusters, such as those created by foundation species, cannot be explained by simple pairwise interactions but request an understanding of the higher order interactions (Levine *et al.*, 2017), such as the role of pollinators in interactions among plants.

Material and methods

Experimental setting

A selective removal experiment was performed in the Sierra Nevada Mountains (Loma del Mulhacén, Spain) during July 2015. The study site is located at 3200 m a.s.l. (Lat 37.041417N, Long -003.306400W), characterised by a patchy alpine vegetation dominated by the cushion-forming species *Arenaria tetraquetra* ssp. *amabilis* (Bory) H. Lindb. Fil. (Caryophyllaceae) and *Hormathophylla spinosa* (L.) Kupfer (Brassicaceae). These foundation species provide positive facilitative effects on other beneficiary plant species through the improvement of their physiological status (Schöb *et al.*, 2012) and reproductive output (Schöb *et al.*, 2014b). These facilitation mechanisms are due to the decrease of stress followed by the increase of soil water content and organic matter in foundation species compared to bare ground (Schöb *et al.*, 2013a,b).

Our null hypothesis is that facilitation influences pollination. Our null expectation is that the pollinator community in a facilitative system is the sum of the components of the facilitative system (i.e., foundation species and beneficiary species). Therefore, we considered the naturally-occurring facilitation clusters with foundation species and beneficiary species as control. In the removal treatment we either removed the foundation species (to have the beneficiary species growing alone) or we removed the beneficiary species (to have the foundation species growing alone).

Each treatment consisted of a standard plot size of 20 x 20 cm. Distance among plots within block ranged between 0.5 m and 1 m. We followed a randomised block design, where each block was composed by foundation species and beneficiary species growing separately and foundation species and beneficiary species growing together replicated over the two foundation species (Figure 1). In total, 14 blocks were established within a relatively homogeneous area of about 1 ha, resulting in 84 plots in total. Plant species composition is the same overall and was kept as similar as possible between treatments of the same block (Tab. SI4).

Plant–pollinator interactions were observed during the entire flowering season of July 2015. Thanks to an exceptionally dry spring and a warm summer, plants completed their flowering phase within three weeks during July. Hence, we were able to cover the complete flowering time for most of the species at our study site. Each plot was sampled during a standardised time span of 20 min a day. The three plots belonging to the same block were sampled together,

in order to eliminate within block variability due to sampling weather conditions. Every day 14 sampling rounds were carried out between 10 am and 5.30 pm (blocks randomly sampled). Each block was sampled between 6 and 9 times, resulting in 204 sampling rounds in total (Tab. SI5).

All flower-visiting insects of each flower (plant species) in each plot were sampled using a sweep net or an entomological aspirator. Thus, pollinator specimens were attributed to a specific plant species within each plot (Tab. SI6). Due to conservation issues related to Sierra Nevada National Park legislation and also ethical issues, we limited the collection of bees, bumblebees, hoverflies and butterflies to those necessary for species identification. Insects were identified at the species level whenever possible, otherwise to genus or family (Tab. SI6). As not all the flower-visiting insects are actual pollinators, we excluded from the analysis all the not-pollinator species. Insect specimens are stored at the ETH insect collection and at our private collections.

Network analysis

To assess wether the observed community is different from the sum of its single components, we compared pollinator communities visiting the observed facilitation clusters with foundation and beneficiary species (i.e., control, 'facilitation' treatment in Figure 1) with the expected additive pollinator communities calculated as the sum of the species growing alone. We highlight that the comparison of the observed facilitation clusters to the sum of its components is a more conservative approach than that of a mean of the components as we have double the area for the expected community. However, we believe that this approach is not only more conservative but also more accurate because we keep the number of plants and flowers similar among treatments.

Pollinator diversity was calculated with the Shannon index (Oksanen *et al.*, 2017) at the plot level. As pollinator abundance responds to flower density (Losapio *et al.*, 2016), visitation rate of each plant species was calculated by standardising the number of pollinators by the number of flowers and sampling hours at the plot level.

Then, we considered the pollination networks at the treatment level. network architecture was calculated according to the measure of nestedness by Bastolla *et al.* (Bastolla *et al.*, 2009). We chose this metric instead of NODF because the latter does not accurately consider the contribution of different species with the same degree to network nestedness, which in our case is fundamental given the long tail of pollinators with few visits per plant species. This nestedness was calculated as $\eta = \frac{1}{2}(\sum_{i<j} \frac{n_{ij}^{pl}}{min(n_i^{pl},n_j^{pl})} + \sum_{i<j} \frac{n_{ij}^{pol}}{min(n_i^{pol},n_j^{pol})})$ where n_{ij} is the number of interactions n between two plant (pl) or two pollinator (pol) species i–j and $\min(n_i, n_j)$ is the smaller of the two values.

To estimate the significance of each observed network, we compared the observed index with the distribution (95% confidence interval) of 100 random networks (Tab. SI4). Random networks were built according to a probabilistic null model (Bascompte *et al.*, 2003), which does a relative good job in minimising simultaneously Type I and Type II errors (Rodríguez-Gironés & Santamaría, 2006) and it is most biologically meaningful in terms of species generalisation

(i.e., node degree). This null model builts networks from a template of interaction probabilities, such that in an adjacency matrix $A = R \times C$ with R and C rows and columns, respectively, the probability that a cell a_{ij} has a link is $\frac{1}{2}(\frac{a_i}{C} + \frac{a_j}{R})$ where a_i and a_j is the number of links in row i and column j, respectively. Only random networks with R and C equal to the empirical networks were considered.

To compare nestedness between facilitation and additive networks, we controlled for the variation in matrix size (R, C) by calculating the deviance of the empirical nestedness with the random expectation given by the 100 replicates of the probabilistic null model as $Z = \frac{o-r}{sd(r)}$, where o and r are the values of epirical and random networks, respectively, weighted by the standard deviation sd of random networks.

Second, we focused on the networks composed by the species common to both treatments.

We first decomposed network dissimilarity (Fig. SI3) into species turnover and interaction rewiring components using the β-diversity of interactions approach (Poisot *et al.*, 2012).

Thus, to exclude differences between networks due to changes in species composition we built networks considering only shared species between treatments (Figure 12). To estimate interaction rewiring, we then calculated both the species-level and network-level diversity of interactions using the Shannon index (Oksanen *et al.*, 2017).

To assess the functional consequences of such interaction rewiring we computed the robustness of networks against secondary extinctions. In absence of biologically-informed criteria of species susceptibility to environmental perturbations (Losapio & Schöb, 2017), we proceeded considering a scenario of random extinction of species, a scenario of extinction in order of most specialised plants and a third of most specialised pollinators (Albert & Barabasi, 2002; Dunne *et al.*, 2002; Solé & Montoya, 2001). Robustness was calculated as the area under the secondary extinction curve generated by sequential removal of plant and pollinator species in random order (Dormann *et al.*, 2009). Each series was replicated 100 times. Each empirical value was compared to a distribution (95% confidence interval) of 100 random networks (Z-score).

Statistical analysis

Regression models were used to assess the effect of treatment (additive vs. facilitation), foundation species (i.e., *Arenaria* or *Hormathophylla*) (predictors) and their interactions on pollinator diversity, relative nestedness (responses, two different models). To assess changes in pollinator visitation rate and interaction diversity (responses) a mixed-effect model approach was used fitting species identity as random term and treatment and foundation species as fixed effects. To assess differences in network robustness (response) a mixed-effect model was fitted using extinction scenario, treatment, foundation species and their interactions as predictors and the random network as error term. The effect of network-level interaction diversity (predictor) on relative robustness (response) was tested using a regression model with the interaction terms interaction diversity–treatment and interaction diversity–foundation species for each scenario separately. To assess the significance of specific contrasts, Tukey HSD post-hoc tests and comparisons among least-squares means (with Tukey correction) were performed on each statistical

model. All data analyses were performed in R version 3.3.3 (R Core Team, 2017).

Acknowledgements

This study was supported by the Swiss National Science foundation awarded to CS (PZ00P3_148261). JB is supported by the European Research Council through an Advanced Grant. We thank L. Dutoit for helping with data collection, M. Furler for drawing Figure 1 and the Sierra Nevada National Park for providing sampling permissions. Thanks to Hannes Baur, Andreas Müller and Martin Schwarz for helping with species identification.

Data accessibility

All original data used in this study will be available from the Dryad Digital Repository. **R scripts** will be uploaded as online supporting information.

Supporting Information

Additional supporting information may be found in the online version of this article.

Author contributions

G.L. and C.S. designed and performed the experiment; G.L., M.A.F., J.B., B.S., R.M. and C.S. discussed methodological issues and results; R.N., H.B., L.C., P.C., C.G., J.P.H., S.K., A.M., J.O., A.C.P., P.R., J.S., M.S. and D.S. contributed to species identification; G.L. analysed the data with input from M.A.F. And J.B.; G.L. wrote the first draft of the paper and all authors contributed to the subsequent revision. The authors declare no conflict of interest.

Conclusion

We have progressively lost contact with Nature,
which is our home and we are of it, not above it.
— Stuart A. Kauffman

After four decades of emphasis on competition and predation, in the last years we are appreciating the power and creativity of positive interactions. On one side, facilitation offered novel insights into the nature of plant communities (Callaway, 2007; Pugnaire, 2010). On the other side, mutualistic networks advanced our understanding of the architecture of biodiversity (Bascompte & Jordano, 2007, 2014). Nevertheless, these two fields have evolved in parallel. Now, we are bridging research on plant facilitation and mutualistic networks into a unified framework.

In this thesis we seek deeper, integrative understanding to questions related to the relationships between species interactions and biodiversity, ecological networks and environmental change, plant facilitation and pollinators. Our original work touches a broad range of fields, from complex sciences to community ecology. Specifically, we explored the emergent nature of plant communities and mutualistic networks resulting from plant–plant interactions. Research has been empirical and computational, analytical and conceptual.

In chapter one we explored the hypothesis that ecosystems are structured by networks of interactions among plant species. In particular, we aimed to unravel the functioning of plant interaction networks, the mechanisms underlying their origin and their dynamic across spatial scales. By using a novel approach that integrates spatial pattern analysis, the ecology of plant interactions and network theory we discovered that plant communities are organised in spatially variable and complex networks. We found that facultative positive plant interactions promote the formation of complex networks at small spatial scale thanks to a cascade of facilitative interactions. In summary, this study highlights the importance of positive interactions for biodiversity and ecosystem stability by use of a novel original framework to analyse ecological networks across scales. Furthermore, our original research findings of a scale-dependent change in network structure are novel and of general interest for both theoretical and empirical ecologists, hence contributing to new conceptual developments in ecology and evolution.

In the second chapter we aimed to assess the impact of three environmental change scenarios on the robustness of a plant–plant network. We developed a new analytical and conceptual framework that links functional traits, environmental change, network theory and species extinction models. We recorded abundance and functional traits of individual plants associated with three foundation species and growing alone. Using a functional trait-based criterion for species susceptibility to each environmental change scenario, we simulated primary species loss and explored the network robustness against secondary extinctions. One simple conclusion that we could draw from this work is that network robustness and species loss depended on the main driver of environmental change. The reason is that the network was more robust

to drought increase and more fragile to increasing nitrogen deposition in our study system, i.e., a dry ecosystem. Our results of a context-dependent robustness of the network is highly relevant for predictions of the fate of plant communities in a changing environment, as they highlight the need to know the sensitivity of the prevailing plant community to main drivers of environmental change.

In the last chapter we explored the hypothesis that plant–plant interactions drive the assembly of mutualistic communities. In particular, we aimed to unravel how the bottom-up effects of facilitation among plants shape the architecture and robustness of pollination networks. We presented a novel approach that combines unique experimental field work with state of the art network analysis. We discovered that plant interactions could scale up to another trophic level in the ecosystem. Our results demonstrate for the first time that non-additive effects of plant facilitation could shape the architecture and robustness of pollination networks. Particularly, we could reveal that the networks of the observed natural communities were different from the sum of single-network components, a cornerstone of system thinking which has never experimentally been proven in community ecology. Finally, thanks to natural history knowledge we could understand the directionality of these effects.

Taken together, our results contribute to advance the understanding of natural systems and potentially contribute to solve environmental issues. We showed, for the first time, the spatial dynamic of plant interaction networks and the relationships between positive interactions, network cohesiveness and species richness. We provided a novel, biologically-meaningful approach for modelling species extinction in relation to environmental perturbations. Moreover, we found experimental evidence for the propagation of plant facilitation to pollination networks.

Research about plant interaction networks may improve our understanding of how ecosystems will respond to global change, which in turn may help to improve current conservation and restoration practices. Broadly speaking, the findings of non-additive effects of facilitation have great significance for the application of complexity sciences to studies of natural, economical, social and technological systems. The role facilitation plays in the assembly of networks and in the maintenance of biodiversity across different scales has important meaning for life sciences. It might potentially contribute to move the actual cultural background beyond the competition archetype towards positive-interactions-oriented perspectives. Probably, the painting *Exploding flowers* (Fig. 15) by Salvador Dalí (1904–1989) dated 1951 illustrates, with decades in advance, the renovated idea of nature founded on interconnected positive interactions. Time seems now mature to incorporate the overlooked role of positive interactions into mainstream science and human culture.

The conclusion I can draw from this research is that positive interactions matter. They matter for keeping a network cohesive in space and in face of perturbations. They matter for different trophic levels in the ecosystem. They particularly matter if we seek an integrative understanding of different linkages in ecological systems, moving far beyond reductionist studies of pairwise competitive interactions.

The implications of this thesis are important not only for academic researchers but might

Figure 15 Exploding flowers, 1951, Salvador Dalí (1904–1989). Photo credit: pinterest.com.

be relevant for professional ecologists, conservationists, policy makers and educators. The support facilitation provides for network cohesiveness can be used by educators and politicians seeking the importance and the consequences of positive interactions beyond individuals and local community borders. The trait-based model of cascade co-extinctions could be used to draw ad hoc interventions to protect endangered species and restore habitats. Furthermore, by focusing on facilitation and knowing the limiting factor of an ecosystem it would be possible to provide specific solutions to aridification and pollution. The role of facilitation for network structure as well as the synergistic effects of foundation and beneficiary species on pollinators provide formidable examples for organic farmers as well as for facing environmental degradation problems. More generally, these original results are not only interesting for ecology, but beyond. Our findings about the role of clustering and positive interactions on other levels can be important for people working on socio-economic systems.

Limitations

Nevertheless, it is important to trace the limits of this work. The first limitation resides in the restrictions typical of any observational study. Despite the use of advanced statistical techniques with specifically designed data, observational patterns cannot provide any proof of

causes and consequences underlying species interactions. Rather, the inference about processes has to be understood to the domain of proposition and potentiality, as indicator and guidance for the subsequent, necessary demonstration.

Second, such as any kind of model, networks provide an approximation to the 'reality'. Insight into the overall community behaviour is gained at the price of complexity and loss of microscopic accuracy. The former poses problems when predicting the outcome of relevant mechanisms, which becomes unfeasible due to many unidentifiable parameters. The latter obscures the break down into operational units, which might also be potentially useful for analytical purposes.

Third, we used insect visitation as a proxy to pollination interactions, which doesn't necessarily translate into pollen deposition or plant benefits. By doing so, we further assume that all the visits are biologically equivalent, that is they have the same unit. However, each species may have its specific pollination capacity depending on the pollen deposited per individual pollinator.

Fourth and finally, considering species masks individual and population levels, which are the level at which most of selection and evolutionary forces take place. Combining individual-based models with network models might improve the understanding of natural selection, its consequences for species interactions and how ecological networks may drive evolution.

Future directions

The significance of our current work for future research is diverse, as are the unanswered questions arising. When plants are co-occurring they are sharing space. We can argue that co-occurrence does not directly translate into interactions. Nevertheless, if the correct scale relevant to species ecophysiological processes is considered, it may be possible to derive an approximation for an assumed *interaction space*. Such approximation may represent the idealised outcome of, for instance, spatial interactions. However, even in the case of appropriate spatial scale contemplation, only from observed co-occurrence it remains hard to quantify the exact nature of the interactions.

Indeed, different interactions are usually concurring over different scales. For instance, co-occurring plants can compete for light, protect each other against frost and not interact for soil nutrients. Consequently, co-occurrence alone cannot furnish any indication about the inherent interaction mechanisms.

We could show a transition from facilitation to competition with increasing spatial scale. This result suggests that both interaction types occur along a continuum. Yet, it is not known to what degree competition and facilitation can coexist in the same system. Experimental manipulation of communities coupled with molecular and biochemical techniques would help to find the physical underpinnings of plant interaction phenomena.

Especially, in order to make significant progress it would be essential to directly quantify plant–plant interactions in their relative context as well as considering different scales. Remaining in the domain of vagueness due to the absence of experimental proof, ecology of species

interactions may incur in the risk of lacking a fundamental body of scientific laws.

Finally, it is probably time to abandon the simplistic abiotic–biotic dichotomy. Light, temperature and water are fundamental aspects for plant life, which are reasonably considered as abiotic factors given their electromagnetic and molecular nature. Nevertheless, if a shading tree reduces light intensity and temperature and increases humidity, can these factors still be considered as purely abiotic? And if an entire tropical forest biome shades and transpires water to the atmosphere for hundreds of squares kilometres, can biotic factors still be considered as only locally important and globally irrelevant?

Complex network approaches can advance our knowledge of life sciences. Shifting the focus from the autoecology and ecophysiology of single, isolated species to the relationships among species represents a deep paradigm change in ecology. Indeed, by overcoming the incorrect assumption of treating species as disconnected entities, network theory is changing the way we approach ecology (Bascompte & Jordano, 2007). With networks we can quantify a whole set of interactions among many coexisting species. These interactions can be a much better indicator of the richness and diversity of ecosystem functions than a simple list of *taxa* and their abundances. We also learned that facilitation networks are relevant for mediating ecosystem robustness against environmental perturbations. Finally, with networks we can make explicit links among different trophic levels in the ecosystem, understanding how different and apparently not-related species can influence each other across the food web. Therefore, a community-level approach that includes species interaction networks may give a more accurate picture about how an ecosystem is functioning, how resistant and resilient it is to perturbations. Such a network perspective, far beyond pairwise competition, can ultimately solve ecological challenges at the root of the problem for a long-term sustainable nature.

Appendix to chapter one

Soil analysis

To quantify small-scale spatial heterogeneity in soil conditions, soil gravel content was measured in composite samples of three subsamples per 1 m^2 by sieving with a 2 mm mesh. From the same soil samples, we also determined gravimetric soil water content by mass loss after drying at 105°C for at least 72 h and the soil C/N ratio with a CHN analyzer (Leco TruSpec Micro CHN, Leco Corporation, St.Joseph, MI).

Spatial pattern analysis

First, we carried out univariate analyses for each single species distribution. We employed the Ripley K function (Baddeley *et al.*, 2015; Ripley, 1981; Wiegand & Moloney, 2014) (Fig. S4) to test each species' spatial pattern against a complete spatial randomness model (CSR), also known as homogeneous Poisson process (HPP). The CSR model is defined by the intensity function λ, which is approximated as $\lambda = \frac{n}{A}$, where n is the number of points, i.e. The number of individuals of the same species, and A is the observational window. For a CSR model with intensity λ, the expected number of points within a circle of radius r around an arbitrary point i is equal to $\lambda K(r)$.

The empirical K function for a HPP is estimated as

$$\hat{K}(r) = \frac{1}{A} \sum_{i=1}^{n} \sum_{j \neq i} \frac{w_{ij}}{\lambda^2} I(d_{ij} \leqslant r) \tag{1}$$

where A is the area of the window, n is the number of points in the plot, w_{ij} is an edge correction factor (translation correction), I is the indicator function that equals 1 if the distance d between points i and j is less than or equal to the radius of the circle r and 0 elsewhere. Theoretical CSR model has constant intensity throughout the study area and assumes independent point distribution(Illian *et al.*, 2008):

$$K(r) = \pi r^2. \tag{2}$$

To test if each species distribution can be explained by this random model, we performed Monte Carlo tests based on simulation envelopes for the $K(r)$ function (Baddeley *et al.*, 2015) for each r =1 cm along 75 cm (i.e. $\frac{1}{4}$ of the shortest side length of the plot, according with Shen *et al.* (2013)). The empirical $\hat{K}(r)$ of each species was compared with the theoretical envelope, built with 95% CI (i.e. The fifth lowest and the fifth highest simulated values of 199 simulations). All plant species significantly differed from a CSR model (Fig. S5).

Consequently, we fitted three different point pattern process models : i) Poisson cluster, ii) inhomogeneous Poisson, and iii) inhomogeneous Poisson cluster. Then, we evaluated which process best described the spatial pattern of each species.

Poisson cluster

A Poisson cluster process (PC) generates non-independent (clustered) points in a two-step process. First, an HPP of "parent" points is generated with an intensity ρ. Then, each parent point i produces "offsprings" j according to a Poisson distribution. The locations of offsprings is independent and isotropically normally distributed around the parent point i, with mean 0 and standard deviation σ. The theoretical K function for a PC is

$$K(r;\rho;\sigma) = \pi r^2 + \frac{1 - e^{\frac{-r^2}{4\sigma^2}}}{\rho} \tag{3}$$

The empirical K function is the same as for HPP (*Eq.*1).

Model fitting involves iteratively choosing the parameters ρ and σ that minimise the discrepancy measure $D(\Theta)$:

$$D(\Theta) = \int_0^{r_0} w(r) \left[\{\hat{K}(r)\}^c - \{K(r;\sigma)\}^c \right]^2 dr \tag{4}$$

where r is the vector of r values at wich the K function is estimated, $\hat{K}(r)$ and $K(r;\sigma)$ are the empirical and the theoretical K functions, respectively, r_0 is the maximum radius r for which the K function has been computed, the weighting function $w(r)$ and the constant c are used to control for sampling fluctuations in $\hat{K}(r)$. According with Diggle (2003) we set $w(r) = 1$ and $c = 0.25$.

Inhomogeneous Poisson

An inhomogeneous Poisson process (IPP) shares with CSR the independence of points but in contrast to CSR its intensity λ is not constant. In IPP λ varies from place to place in the study area according to an intensity function $\lambda(\upsilon)$ assumed to be caused by environmental heterogeneity (Baddeley *et al.*, 2000; Getzin *et al.*, 2008; Wiegand *et al.*, 2007; Wiegand & Moloney, 2014). Hence, IPP is considered as a generalisation of a deterministic niche process. The inhomogeneous K function is (Baddeley *et al.*, 2000):

$$K_I(r) = \pi r^2 \tag{5}$$

and its estimate is:

$$\hat{K}(r) = \frac{1}{A} \sum_{i=1}^{n} \sum_{j \neq i} \frac{w_{ij}}{\lambda(x_i)\lambda(x_j)} I(d_{ij} \leqslant r) \tag{6}$$

The intensity function λ of each species was estimated as a log-linear function of the measured environmental covariates using the *ppm* function of *spatstat* (Baddeley *et al.*, 2015). These spatial covariates were both biotic and abiotic ecological factors with a known role in species distribution and species interactions (Fortunel *et al.*, 2016; Lauber & Wagner, 1996; Shipley *et al.*, 2012; Silvertown, 2004): soil gravel content, soil water content, soil C/N ratio, plant height, plant biomass (calculated as the leaf dry mass x number of leaves), distance to nearest *Dryas octopetala* patch (i.e., the ecosystem engineer of our study system), moss diameter (i.e., indicator of surface runoff), *Saxifraga aizoides* biomass (i.e., indicator of surface runoff and strong competitor), *Anthyllis vulneraria* biomass (legume), *Oxytropis jacquini* biomass

(legume). For producing covariate maps, soil gravel content, soil water content and soil C/N ratio maps were produced with ordinary kriging, while the other covariate maps were produced with kernel smoothing (Fig. S6). A stepwise-selected model procedure by AIC was carried out to fit the best log-linear model for each species.

Inhomogeneous Poisson cluster

An inhomogeneous Poisson cluster process (IPC) is an extension of the PC with, in addition, the distribution of points is assumed to be heteregeneous. The null expectation of the inhoomogeneous K function of an IPC is:

$$K_I(r) = \pi r^2 + \frac{1 - e^{\frac{-r^2}{4\sigma^2}}}{\rho} \tag{7}$$

The empirical $\hat{K}(r)$ function is computed as for an inhomogeneous point pattern (*Eq.*4). Model fitting involves iteratively choosing the parameters ρ and σ that minimise the discrepancy measure $D(\Theta)$ but based on the inhomogeneous K function (*Eq.*3) (Waagepetersen, 2007).

Null model selection

The overall fit of each process was evaluated with the goodness-of-fit υ statistic (Diggle, 2003; Loosmore & Ford, 2006):

$$\upsilon = \int_{r=0}^{r_{max}} \{\hat{K}(r) - \overline{K}(r)\}^2 dr \tag{8}$$

where $\hat{K}(r)$ is the estimation of Ripley's function K of each null model (*Eq.*1,*Eq.*4) for each plant species, $\overline{K}(r)$ is the mean of the theoretical K functions of each null model (*Eq.*3,*Eq.*5,*Eq.*7) over the 199 simulated patterns, r is the range of spatial scales at which the functions are estimated (from 1–75cm with 1 cm steps). After adjusting and evaluating all the three models, the null model with the smallest υ was selected as the best null model to predict the distribution of each species (Fig. S7, Table S2).

All analyses were conducted in R 3.3.0 (R Core Team, 2017), using *spatstat* (Baddeley *et al.*, 2015) and *ecespa* (De la Cruz, 2008).

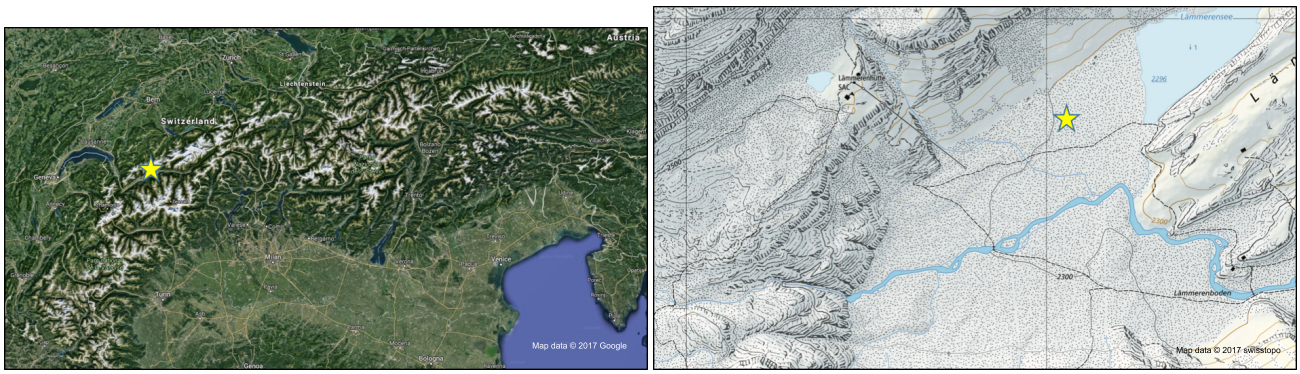


Figure S1 Position of the study site (left) in the Swiss Alps and (right) on the Lämmerenboden (Wallis) area.

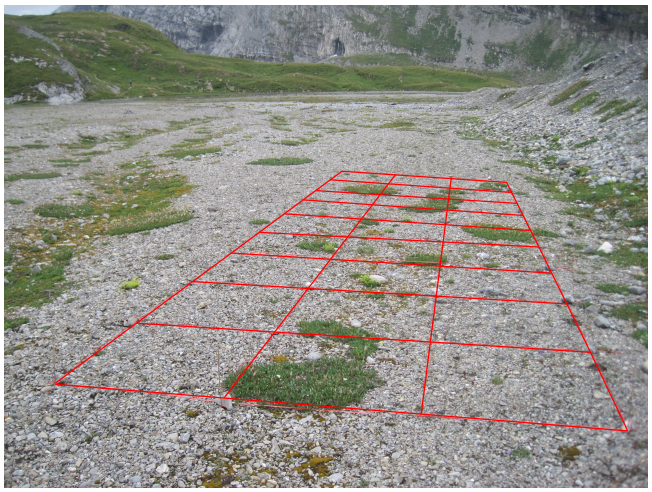


Figure S2 Study site with the 9 x 4 m grid.

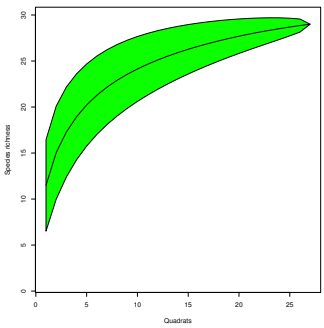


Figure S3 Species accumulation curve of the sampled community.

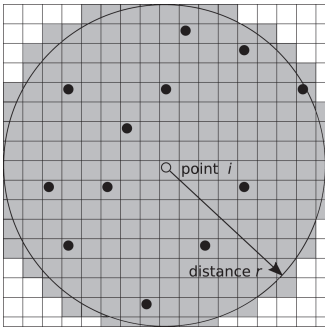


Figure S4 Ripley's K function counts the number of points inside the part of the circle with radius r (i.e. within a distance r) around a point i (modified from Wiegand & Moloney (2004)). Grid spacing is 1 cm.

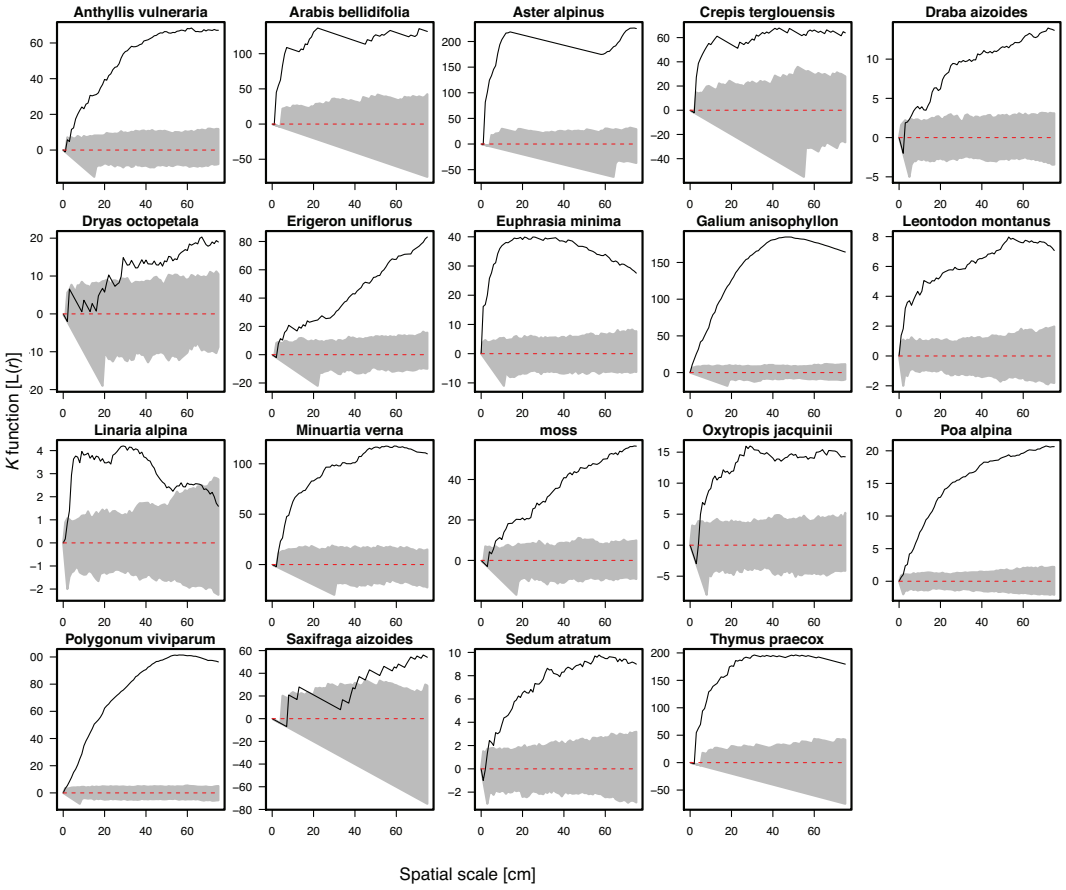


Figure S5 Complete spatial randomness (CSR) models of species distribution. To better interpret the K function visually, we used the L transformation $L(r) = \sqrt{\frac{K(r)}{/pi}} - r$ for plotting (y-axis). All observed black lines significantly lie outside each envelope, indicating intraspecific aggregation and spatial heterogeneity.

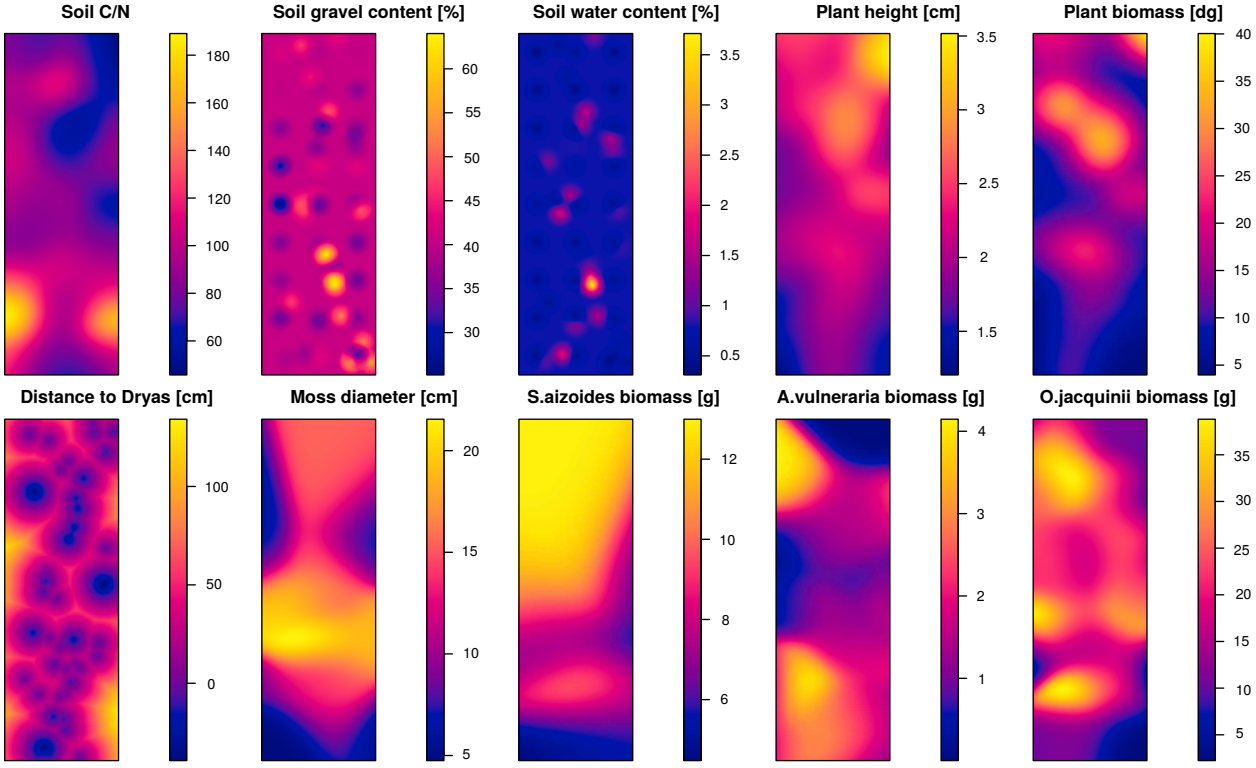


Figure S6 Covariate maps used to fit inhomogeneous point process (IPP) models.

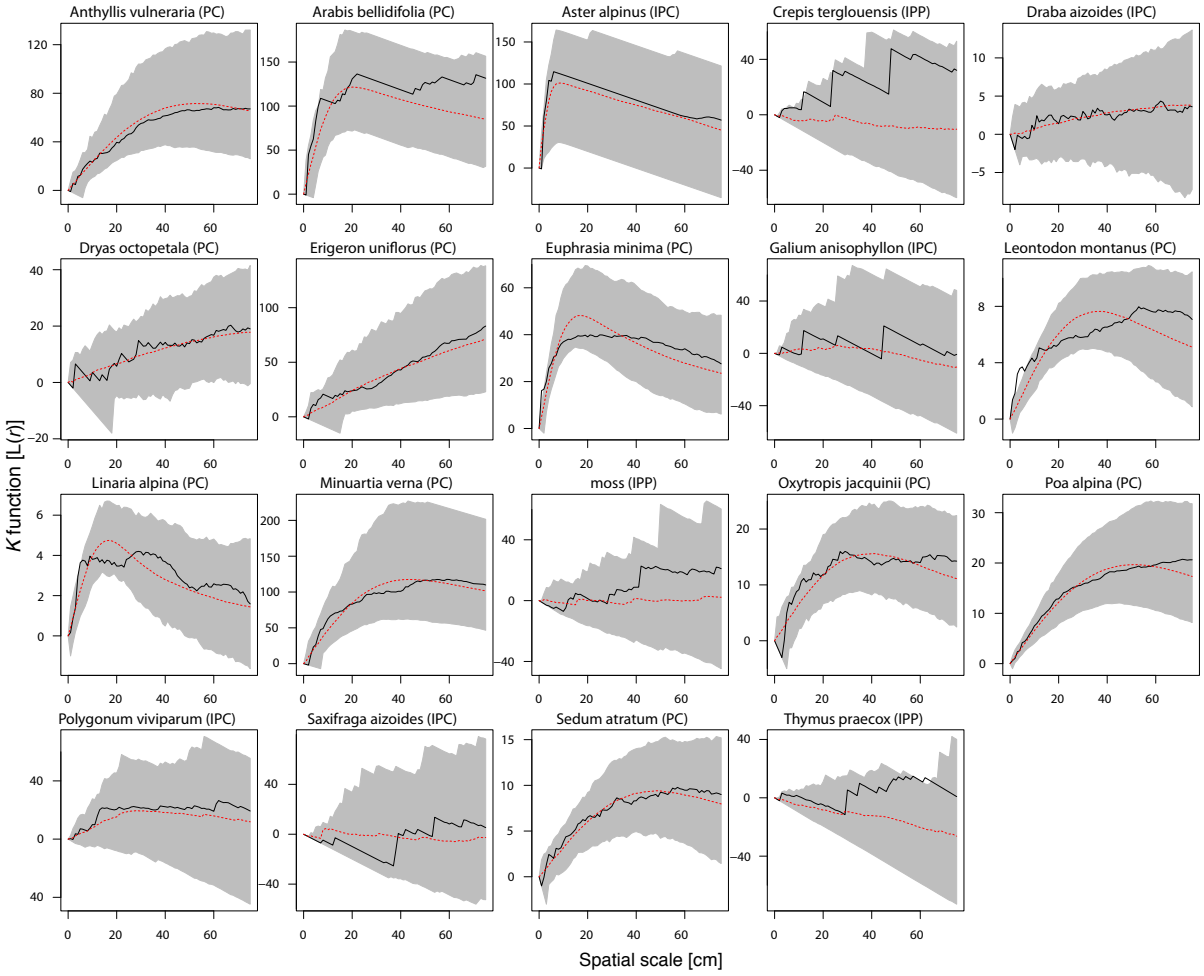


Figure S7 Best null models among inhomogeneous point process model (IPP), inhomogeneous Poisson process (PC) and inhomogeneous Poisson cluster process (IPC) for univariate species distribution. To better interpret the K function visually, we used the L transformation $L(r) = \sqrt{\frac{K(r)}{\pi}} - r$ for plotting (y-axis).

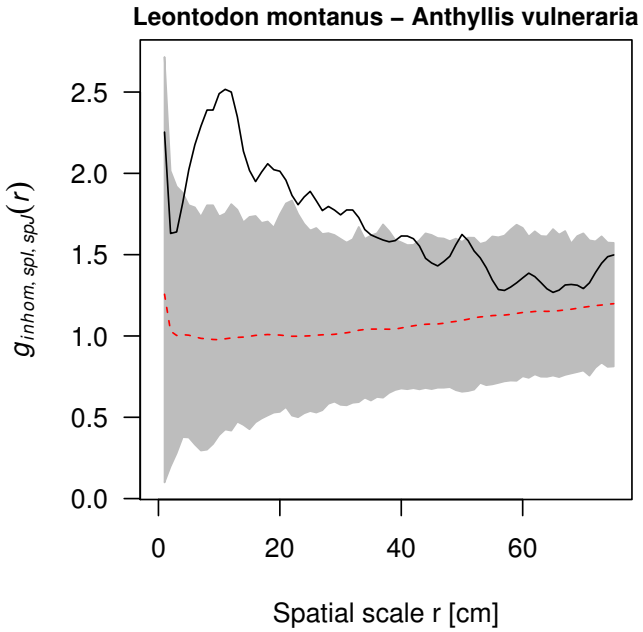


Figure S8 Example of the cross-type pair correlation g function (y-axis) considering the conditional distribution of *Anthyllis vulneraria* (species j) associated to *Leontodon montanus* (species i). Between *c.* 3 cm and 40 cm *A. vulneraria* is significantly positive spatial dependent (i.e., facilitated) on *L. Montanus*.

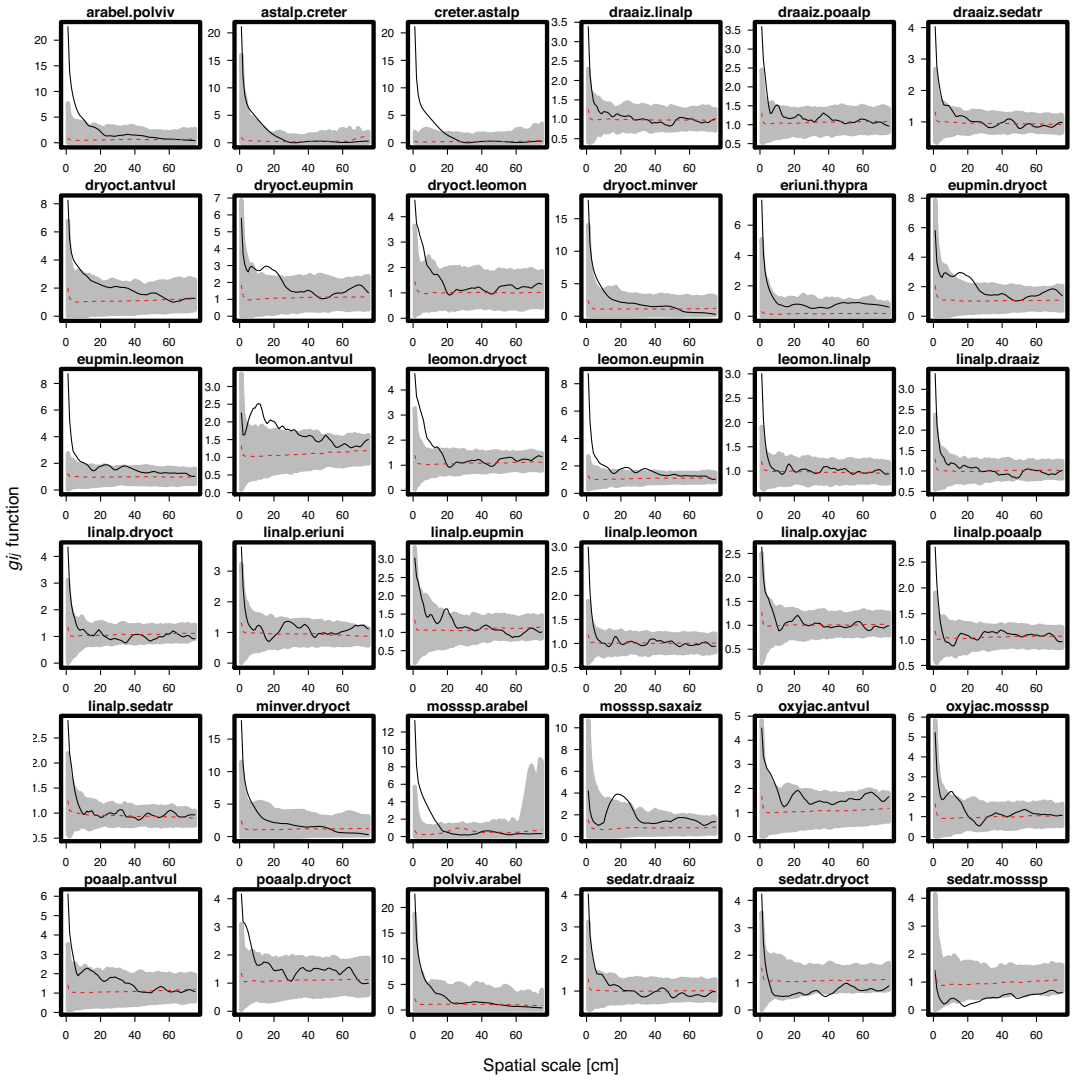
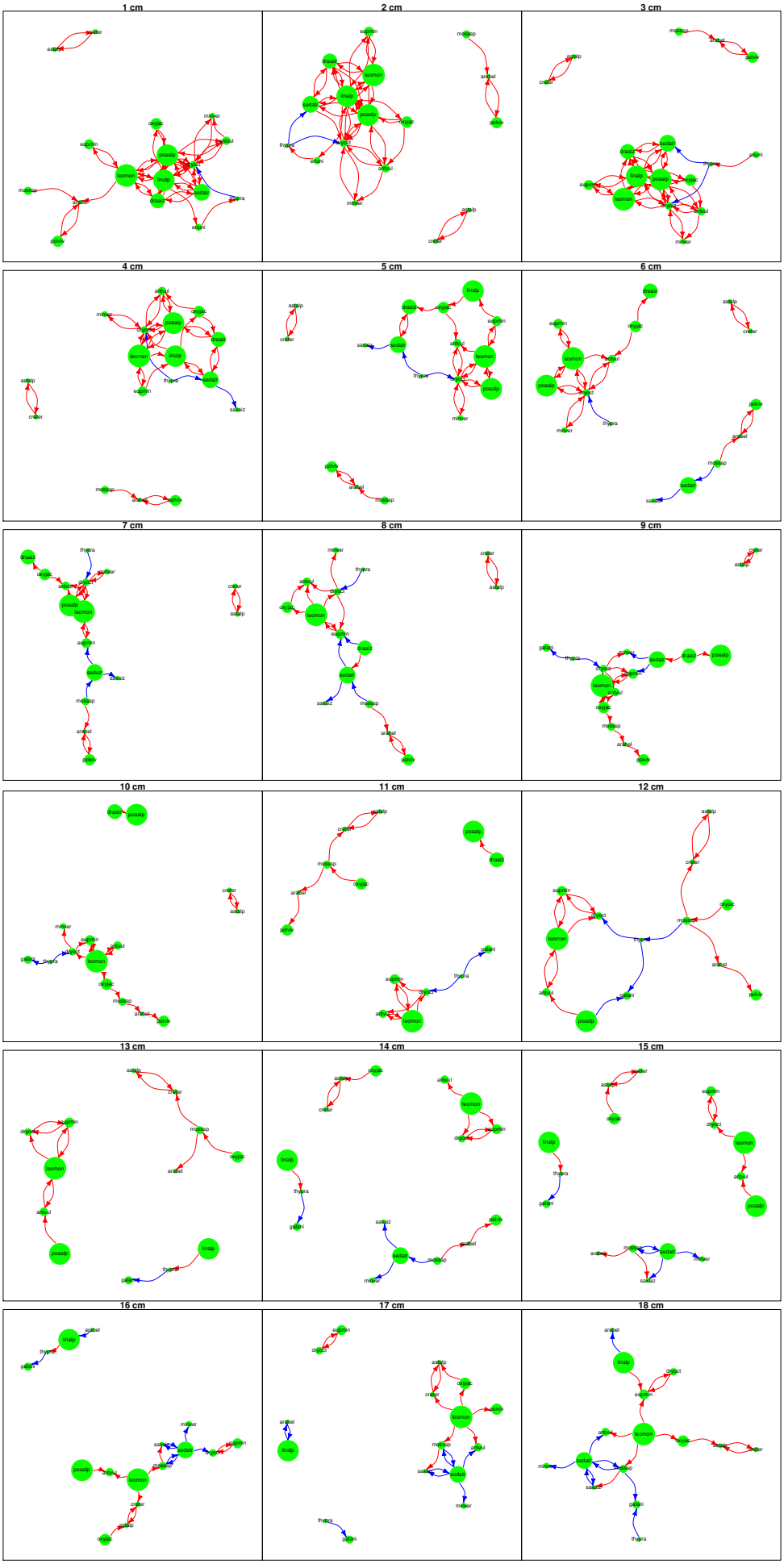


Figure S9 Cross-type pair correlation g function (y-axis) for significantly associated species across the whole spatial scale range (x-axis). For species abbreviations, see Tab. S1.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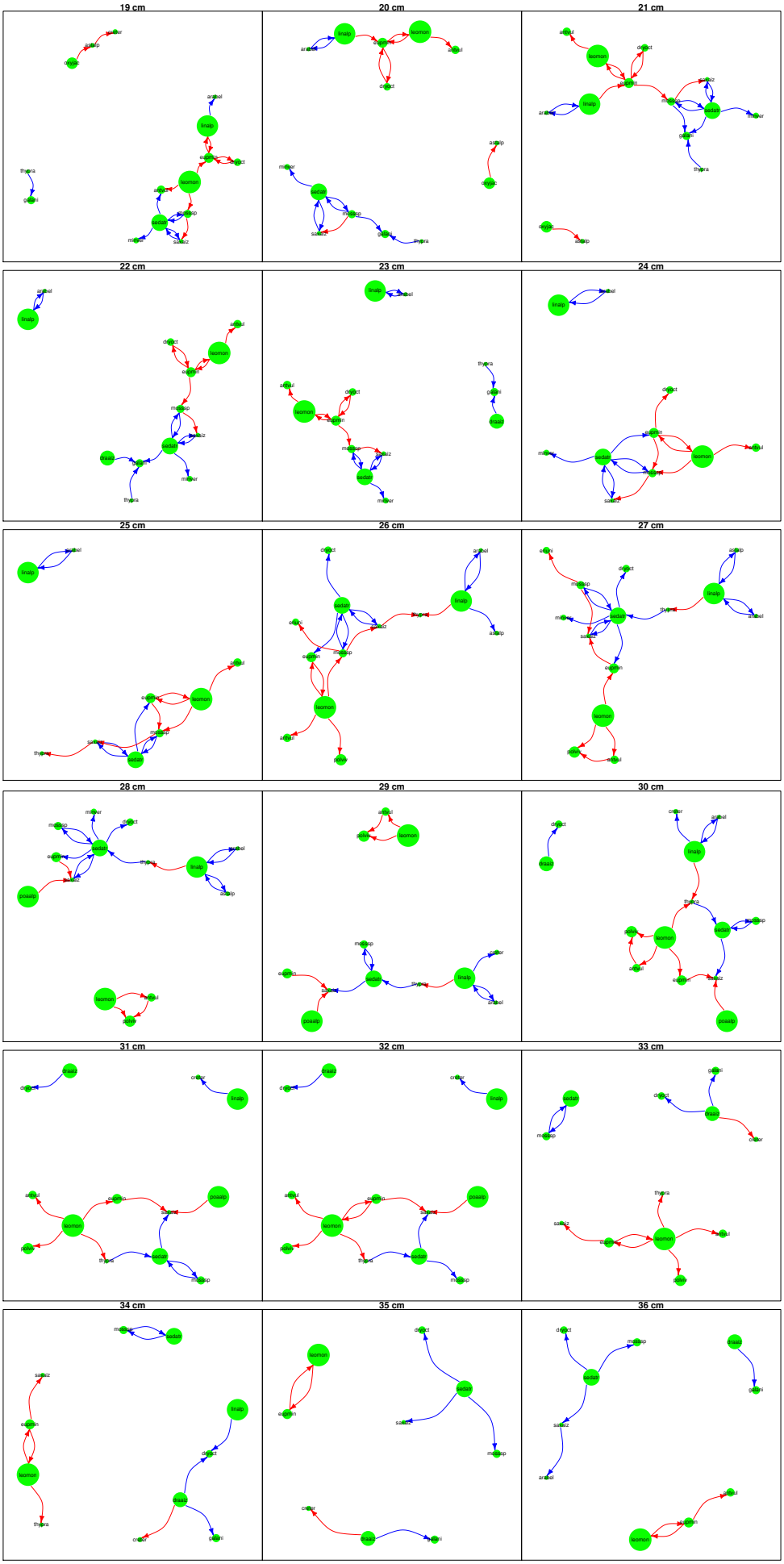
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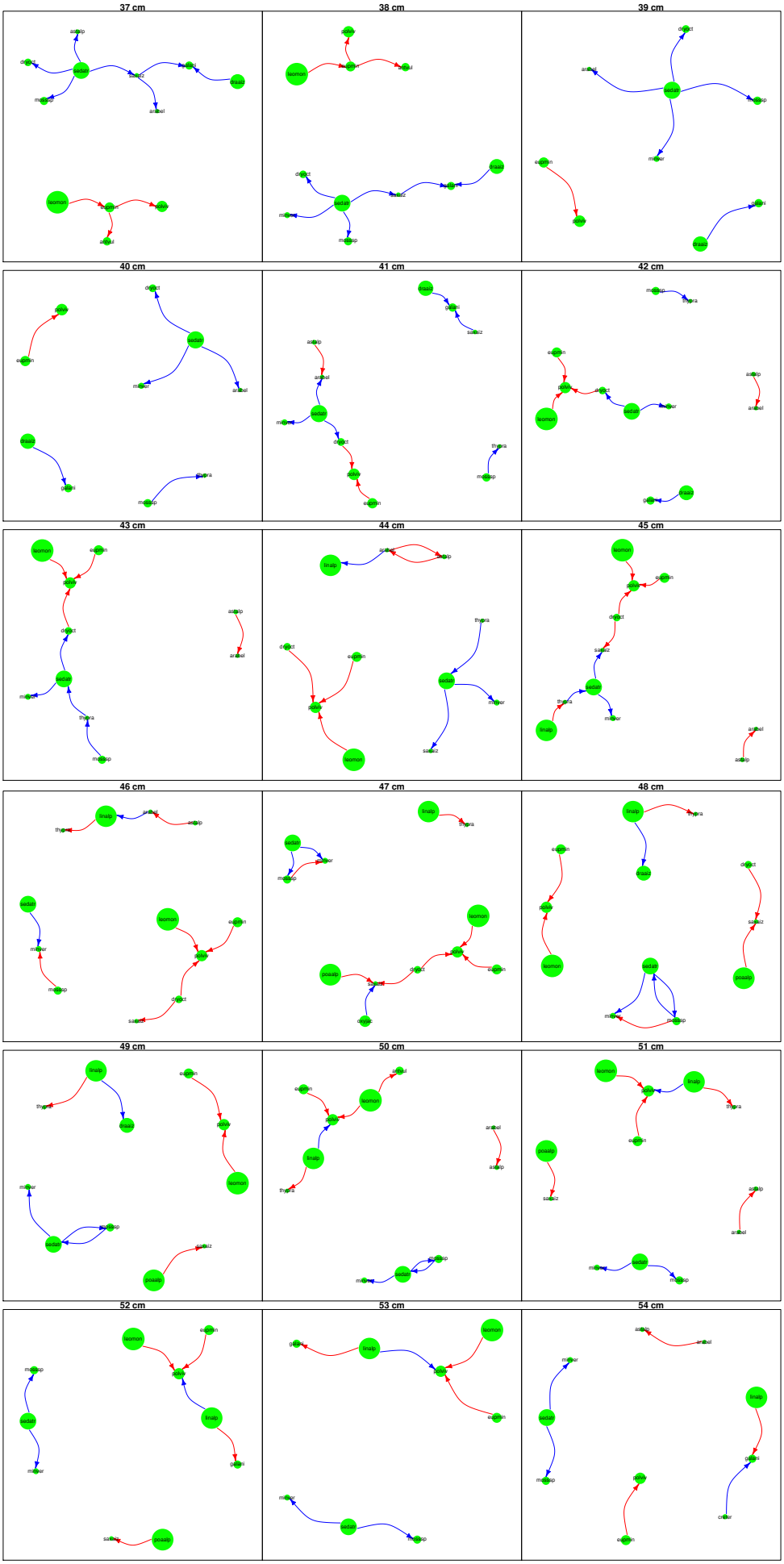
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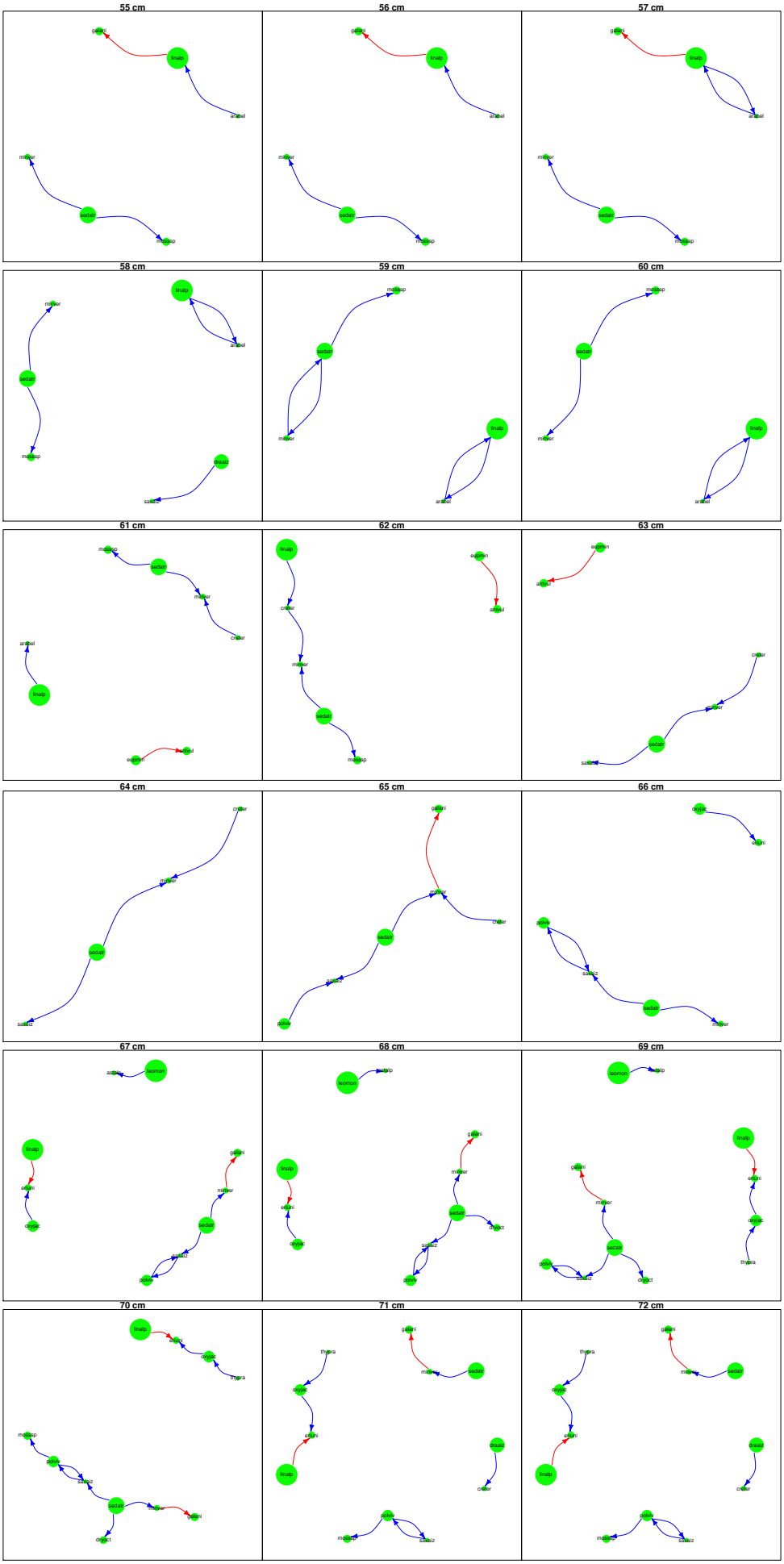
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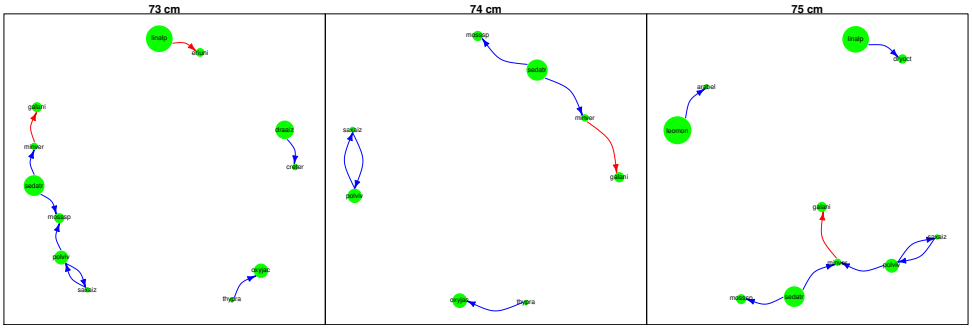

Figure S10 Plant interaction networks across spatial scales. Each node (i.e. A green dot) represents a plant species, with its dimension proportional to its relative abundance (Tab. S1). Arrows represent direct links E_{ij} resulting from $\hat{O}_{ij}$ at each 1 cm scale. Red and blue links depicts positive and negative interactions, respectively (see Video online). For species abbreviations, see Tab. S1.

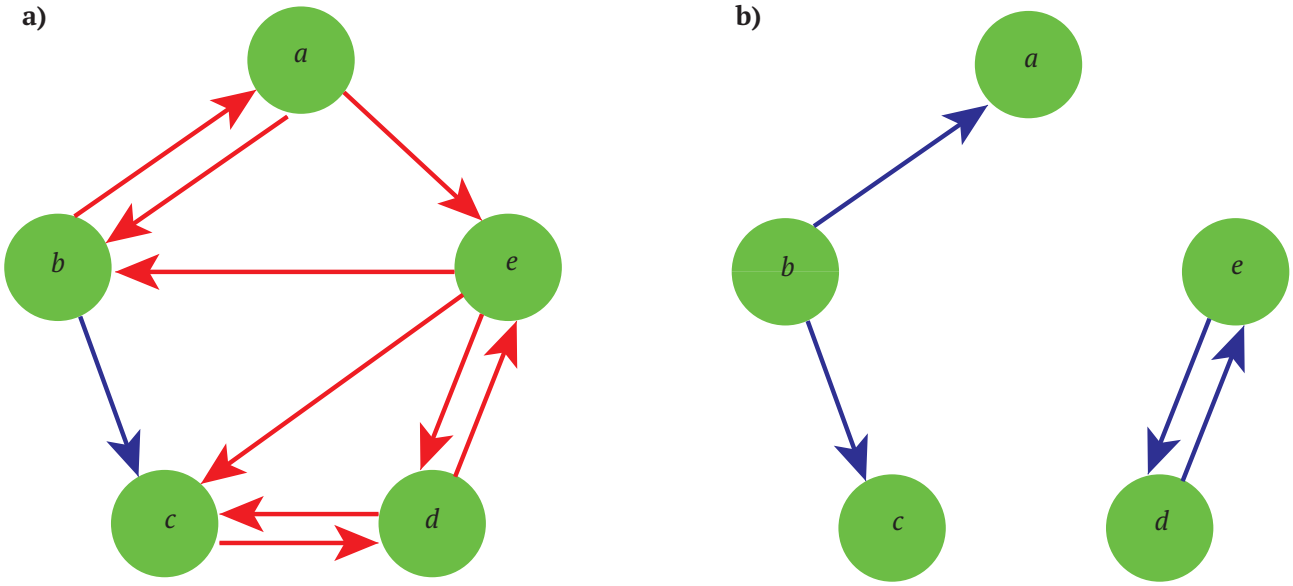

Figure S11 Examples of plant interaction networks: plant species are represented by nodes (i.e. green dots), interactions by arrows, with red indicating facilitation and blue competition. Each community is composed by 5 species (a, b, c, d, e) and: **a)** 10 interactions, of which 6 facilitative mutual (a-b b-a, c-d d-c, d-e e-d), 3 facilitative non mutual (a-e, e-b, e-c), 1 competitive non mutual (b-c); **b)** 4 interactions, 2 competitive mutual (d-e e-d) and 2 competitive non mutual (b-a, b-c). Considering the transitivity: **a)** a has 2 neighbours (b and e), which are linked (b-e), b has 3 neighbours (a, c and e) of which 2 are linked to each other (a-e, e-c) over 3 possible (a-c does not occur), c has 3 neighbours (b, d, e) of which 2 are linked to each other (d-e, b-e) over 3 possible (b-d does not occur), d has 2 linked neighbours (c, e with c-e), e has 4 neighbours (a, b, c, d) of which 3 are linked to each other (a-b, b-c, c-d) over 6 possible (a-c, a-d, b-d do not occur). Hence, network transitivity $C = \frac{1}{5} \times (1(2-1) - 1 + 2(3-1) - 1 + 2(3-1) - 1 + 1(2-1) - 1 + 3(6-1) - 1) = 0.513$; **b)** a has 1 neighbour, b has 2 unlinked neighbours, c has 1 neighbour, d has 1 neighbour, e has 1 neighbour. Hence, network transitivity $C = \frac{1}{5} \times (0(1-1) - 1 + 0(2-1) - 1 + 0(1-1) - 1 + 0(1-1) - 1 + 0(1-1) - 1) = 0$. The size of the largest connected component R (i.e. Number of consecutively linked nodes) is 5 and 3 for **a)** and **b)**, respectively.

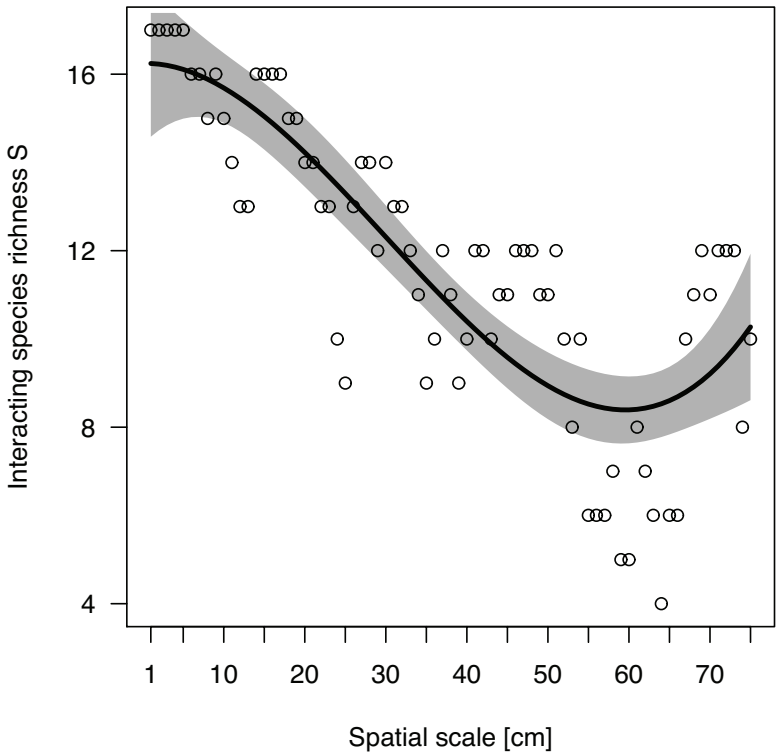

Figure S12 Richness of interacting plant species across spatial scales. The non-linear regression model included the third degree polynomial function of scale as predictor and an autoregressive covariance structure of scale: $\beta = -22.905$, $\beta^2 = 6.937$, $\beta^3 = 4.469$, $p = 0.0004$, $R^2 = 0.642$. Predicted line and 95% CI shown.

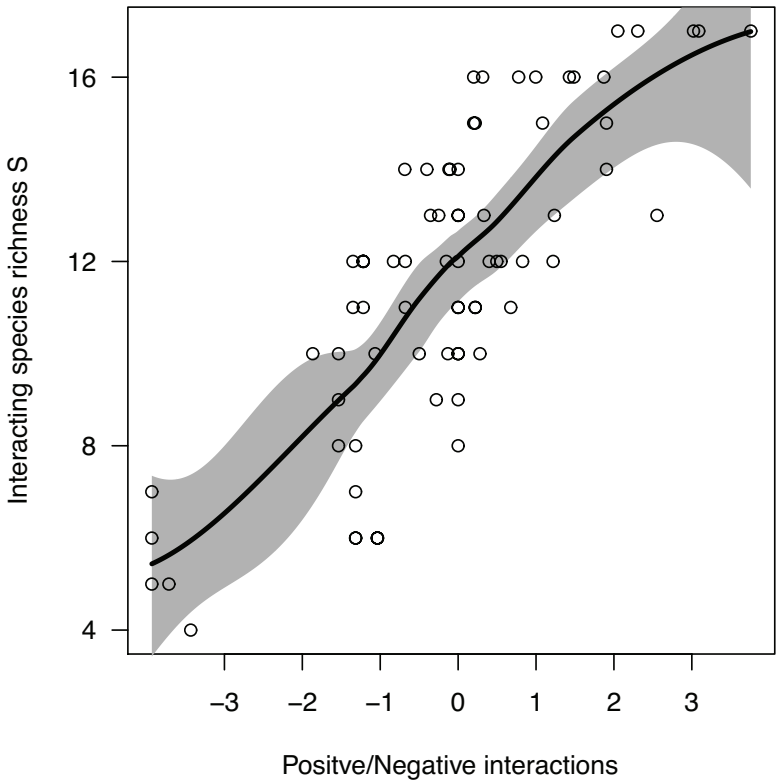

Figure S13 Richness of interacting plant species increased with increasing the relative amount (i.e. log ratio) of positive interactions over negative. The non-linear regression model included the third degree polynomial function of positive/negative interactions (log) as predictor and an autoregressive covariance structure of scale: $\beta = 11.798$, $\beta^2 = -1.800$, $\beta^3 = 4.469$, $p = 0.0019$, $R^2 = 0.270$. Predicted line and 95% CI shown.

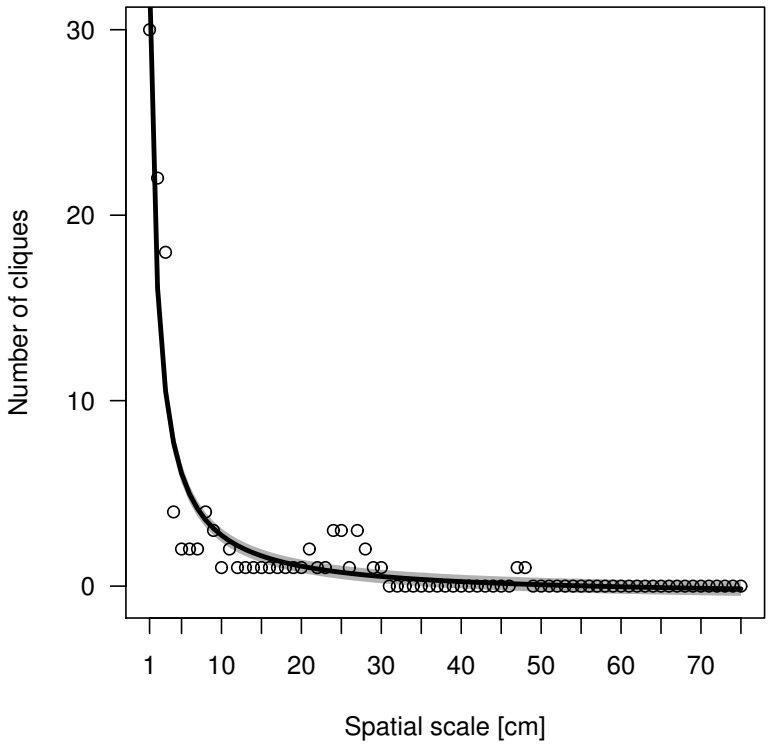

Figure S14 Cliques are small, densely interconnected components, and represent the "substructure" of networks. A clique is a maximally fully-connected sub-graph (i.e., a set species) where every pair of species is connected by a direct link. Here, we consider cliques composed of at least three species and connected by at least one direct link. Hence cliques have important consequences on how processes in the network, as a whole, are taking place (Newman *et al.*, 2006). The number of network cliques exponentially decreased across spatial scales ($\beta = 30.418$, $p < 0.0001$, $R^2 = 0.867$). The number of cliques is significantly affected by both reciprocal ($\beta = 0.679$, $F_{1,70} = 80.35$, $p < 0.0001$) and nonreciprocal ($\beta = 0.374$, $F_{1,70} = 7.19$, $p = 0.0091$) positive interactions, while reciprocal ($\beta = 0.177$, $F_{1,70} = 1.03$, $p = 0.3127$) and nonreciprocal ($\beta = 0.006$, $F_{1,70} = 0.00$, $p = 0.9737$) negative interactions had no significant effect. Predicted line and 95% CI shown.

Table S1 Species list with total number of individuals (Ind) and species relative cover. Only species with more than 10 individuals were considered for the analyses, for a total of 19 species. Taxonomy according to Lauber & Wagner (1996).

Species	**Ind**	**Cover**[%]	**code**
Acer sp.	1	0	acersp
Agrostis alpina	2	0.01	agralp
Anthyllis vulneraria	54	0.51	antvul
Arabis bellidifolia	13	0.02	arabel
Aster alpinus	17	0.13	astalp
Crepis terglouensis	20	0.42	creter
Draba aizoides	171	0.35	draaiz
Dryas octopetala	44	10.04	dryoct
Erigeron uniflorus	39	0.08	eriuni
Euphrasia minima	77	0.04	eupmin
Festuca alpina	8	0.28	fesalp
Galium anisophyllon	51	0.17	galani
Gypsophila repens	1	0.06	gyprep
Hieracium sp.	1	0.01	hiersp
Leontodon montanus	392	2.62	leomon
Linaria alpina	355	1.57	linalp
Minuartia verna	27	0.07	minver
moss	51	2.41	mosssp
Oxytropis jacquinii	103	2.02	oxyjac
Poa alpina	364	2.54	poaalp
Polygonum viviparum	98	0.96	polviv
Pritzelago alpina	3	0	prialp
Salix retusa	4	0.04	salret
Saxifraga aizoides	15	0.36	saxaiz
Saxifraga oppositifolia	7	0.04	saxopp
Sedum atratum	215	0.13	sedatr
Thymus praecox	13	0.03	thypra
Trisetum distichophyllum	5	0.02	tridis
Viola cenisia	3	0	viocen

Table S2 Selection of the best null model among inhomogeneous point process model (IPP), inhomogeneous Poisson process (PC) and inhomogeneous Poisson cluster process (IPC). Differences between theoretical and estimated K functions (v) and their p-values (p) are shown. The smaller the differences, the higher the p-value, the better the pattern estimated from the observed data could be explained by a theoretical function.

Species	**IPP** v	**IPP** p	**PC** v	**PC** p	**IPC** v	**IPC** p	**best**
Anthyllis vulneraria	1.7×10^{10}	0.21	5.4×10^{9}	0.915	3.1×10^{10}	0.275	PC
Arabis bellidifolia	1.1×10^{10}	0.23	4.9×10^{11}	0.31	2.2×10^{10}	0.19	PC
Aster alpinus	1.8×10^{9}	0.315	1.8×10^{11}	0.52	2.7×10^{10}	0.63	IPC
Crepis terglouensis	1.2×10^{10}	0.415	4.1×10^{10}	0.57	1.2×10^{10}	0.715	IPP
Draba aizoides	2.4×10^{9}	0.015	6.3×10^{7}	0.925	1.7×10^{7}	1	IPC
Dryas octopetala	2.5×10^{10}	0.795	2.4×10^{8}	0.995	1.2×10^{9}	0.72	PC
Erigeron uniflorus	1.8×10^{11}	0.06	1.0×10^{10}	0.88	7.6×10^{10}	0.77	PC
Euphrasia minima	2.5×10^{10}	0.055	3.9×10^{9}	0.735	1.8×10^{10}	0.07	PC
Galium anisophyllon	3.3×10^{11}	0.015	1.2×10^{10}	0.995	7.9×10^{9}	0.665	IPC
Leontodon montanus	7.0×10^{8}	0.01	1.6×10^{6}	0.425	2.1×10^{6}	0.425	PC
Linaria alpina	3.8×10^{8}	0.005	2.5×10^{7}	0.685	3.4×10^{7}	0.74	PC
Minuartia verna	4.9×10^{12}	0.005	3.7×10^{10}	0.895	5.5×10^{11}	0.02	PC
moss	2.8×10^{8}	0.995	1.1×10^{9}	0.985	1.9×10^{10}	0.125	IPP
Oxytropis jacquinii	4.0×10^{8}	0.765	3.6×10^{8}	0.735	9.0×10^{8}	0.575	PC
Poa alpina	1.1×10^{10}	0.015	2.6×10^{8}	0.77	4.2×10^{9}	0.65	PC
Polygonum viviparum	8.1×10^{10}	0.06	4.6×10^{10}	0.79	5.1×10^{9}	0.805	IPC
Saxifraga aizoides	2.8×10^{10}	0.405	9.1×10^{10}	0.04	8.3×10^{9}	0.715	IPC
Sedum atratum	1.0×10^{10}	0.005	3.8×10^{7}	0.915	1.8×10^{8}	0.81	PC
Thymus praecox	4.6×10^{9}	0.32	1.9×10^{11}	0.21	1.3×10^{10}	0.13	IPP

Table S3 Results of non-linear models to analyse the change in number of positive and negative interactions (Pos/Neg), reciprocal and nonreciprocal interactions (Rec/Non), total number of interactions (L) and interacting species richness (S). Fixed-effects β included third degree polynomial functions (β: linear/quadratic/cubic terms). In order to account for spatial autocorrelation across scales, an autoregressive covariance structure was included in the model (i.e. AR(1) $\sigma_{ij} = \sigma^2\rho^{|i-j|}$). AR(1) assumes that two measurements that are close in space are more correlated than if these measurements were farther apart. Intercept estimates not shown.

Response	**Predictor**	**DF**	β	β^2	β^3	p-**value**	R^2
Pos/Neg	scale	3,71	-10.29	2.67	-2.42	0.0001	0.607
Rec/Non	scale	3,71	-10.33	6.66	3.61	0.0005	0.590
L	Pos/Neg	3,59	36.09	-21.91	-0.58	<0.0001	0.665
	Rec/Non	3,59	12.55	-6.64	-16.37	<0.0001	
	Pos/Neg:Rec/Non	9,59	386.2	-300.9	-10.7	0.0013	
S	Pos/Neg	3,59	51.29	-32.20	5.94	0.0004	0.630
	Rec/Non	3,59	-18.31	-28.32	-17.99	0.2123	
	Pos/Neg:Rec/Non	9,59	500.21	-551.65.9	-28.44	0.1402	

Table S4 Results of fixed effects models to analyse the change in network transitivity C and size of the largest connected component R. Fixed-effects β included the absolute number of positive reciprocal (Positive-Positive), positive nonreciprocal (Positive-Neutral), negative reciprocal (Negative-Negative), and negative nonreciprocal (Negative-Neutral) interactions. No Positive-Negative nor Negative-Positive interactions occurred. In order to account for spatial autocorrelation across scales, an autoregressive covariance structure was included in the model (i.e. AR(1) $\sigma_{ij} = \sigma^2\rho^{|i-j|}$). AR(1) assumes that two measurements that are close in space are more correlated than if these measurements were farther apart. Intercept estimates not shown.

Response	**Predictor**	**DF**	β	**F-value**	**partial** r^2	p-**value**	R^2
C	Positive-Positive	1,70	0.044	44.57	0.361	<0.0001	0.633
	Positive-Neutral	1,70	0.065	10.54	0.225	0.0018	
	Negative-Negative	1,70	0.026	5.27	0.096	0.0247	
	Negative-Neutral	1,70	-0.089	6.37	0.117	0.0139	
R	Positive-Positive	1,70	1.189	43.96	0.504	<0.0001	0.715
	Positive-Neutral	1,70	2.090	35.34	0.383	<0.0001	
	Negative-Negative	1,70	0.855	2.83	0.161	0.0971	
	Negative-Neutral	1,70	3.810	27.03	0.249	<0.0001	

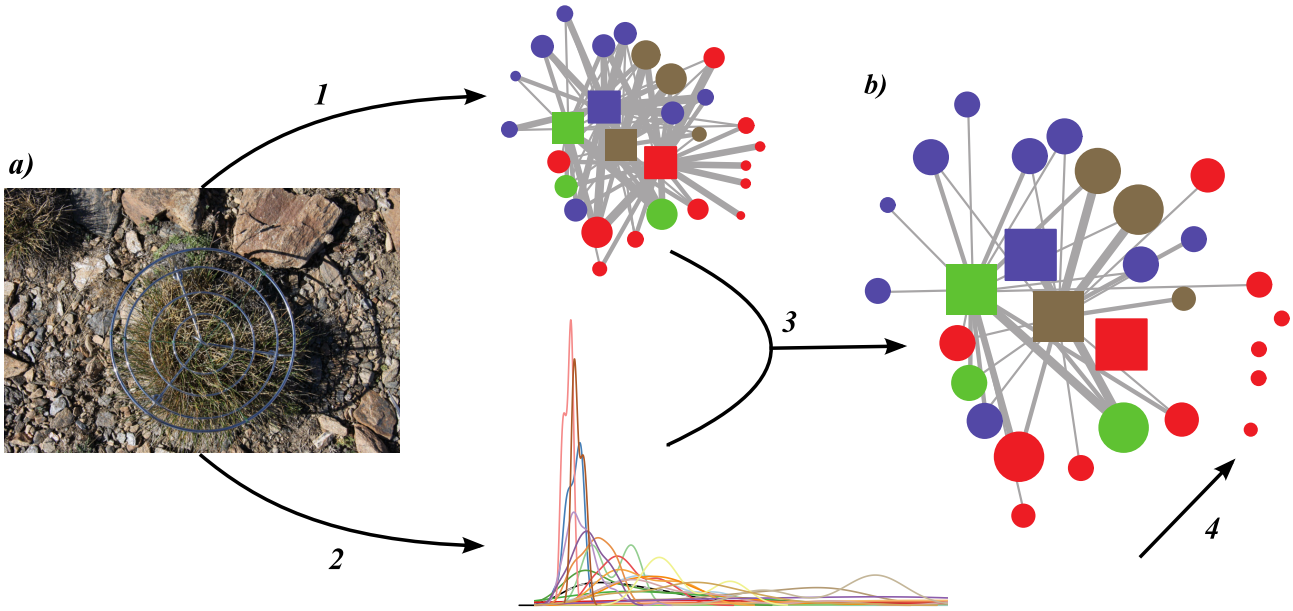

Figure S1 Conceptual framework for assessing plant community persistence against environmental perturbations by implementing the traits of species and their relationships with environmental changes into plant interaction network analysis. Starting from the sampled plant community ***(a)***) we built the corresponding plant association network ***(1)*** and we characterized the species trait distributions ***(2)***. For each scenario, according to the corresponding trait-environment relationship, an increasing number of intervals was removed from the viable trait space. This procedure produced primary extinctions for plant species that did not fit the resulting viable trait space and secondary extinctions for plant species that lost their microhabitat (i.e., the associated foundation species) ***(3)***. For the resulting plant association network ***(b)***) we calculated the number of surviving species and the number of secondary extinctions ***(4)***.

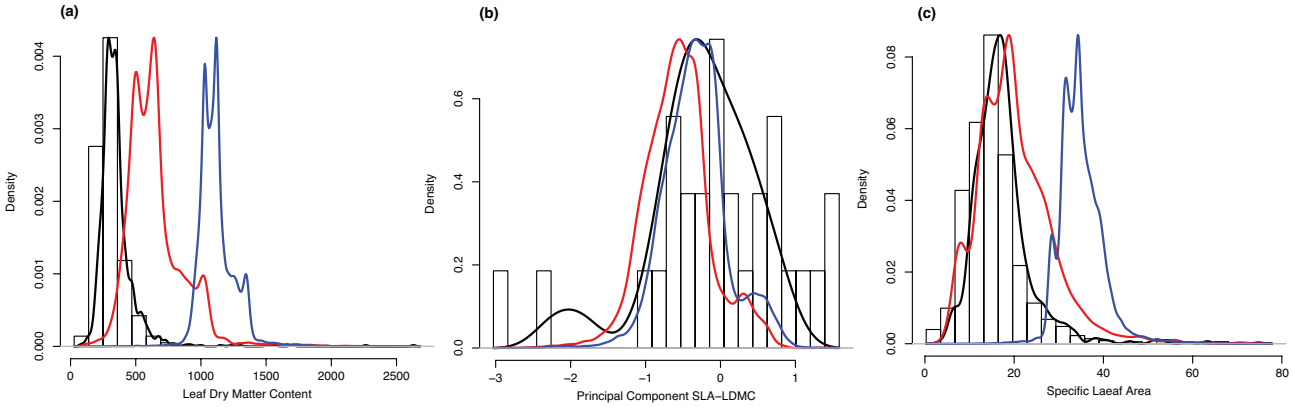

Figure S2 Distribution of observed traits (black lines and bars), simulated traits with 200 replicates (red lines) and with 1000 replicates (blue lines) for all plant species in each scenario. Lines fitted with kernel density estimates.

Table S1 Multinomial log-linear model of the differences among subordinate species in their persistence within the network, i.e. Surviving or getting secondary extinct. Shown are the estimate η (logit) and the confidence interval CI (2.5% and 97.5%). Primary extinction was the reference level (i.e., the intercept, estimates omitted). Positive and negative values indicate an increase or decrease in the likelihood of survival or secondary extinction in comparison with primary extinction, respectively.

Species	**Survival**		**Secondary extinction**	
	η	**CI**	η	**CI**
A.nevadensis	-0.52	-0.55– -0.49	2.04	-2.09– -1.98
A.vulneraria	-1.03	-1.06– -1.00	-2.08	-2.13– -2.03
A.tetraquetra	-0.7	-0.73– -0.67	-2.45	-2.51– -2.39
C.oporinoides	-1.25	-1.28– -1.21	-1.50	-1.54– -1.46
D.brachyanthus	-0.51	-0.54– -0.48	-1.40	-1.44– -1.36
E.glaciale	-0.66	-0.69– -0.63	-2.35	-2.41– -2.29
E.nevadense	-0.58	-0.61– -0.55	-2.32	-2.38– -2.26
E.willkommii	-1.01	-1.04– -0.98	-2.34	-2.39– -2.28
F.indigesta	-0.29	-0.32– -0.25	-1.06	-1.1– -1.02
G.pyrenaicum	-0.56	-0.59– -0.53	-0.85	-0.88– -0.81
J.amethystina	-1.34	-1.38– -1.30	-1.33	-1.37– -1.29
J.humilis	-1.08	-1.11– -1.04	-1.84	-1.88– -1.79
K.vallesiana	-0.62	-0.65– -0.59	-2.50	-2.57– -2.44
L.boryi	-0.92	-0.95– -0.89	-2.75	-2.82– -2.68
L.pectinata	-0.86	-0.89– -0.83	-2.68	-2.75– -2.61
L.corniculatus	-0.85	-0.89– -0.82	-1.51	-1.56– -1.47
N.purpurea	-0.56	-0.59– -0.53	-1.75	-1.80– -1.70
P.holosteum	-0.68	-0.71– -0.65	-2.45	-2.51– -2.39
P.ligulata	-0.15	-0.18– -0.12	-16.41	-85.66– 52.83
R.angiocarpus	-1.38	-1.42– -1.34	-2.09	-2.14– -2.04
S.amplexicaule	0.24	0.22– 0.27	-16.24	-86.38– 53.91
S.boissieri	-0.62	-0.65– -0.59	-2.5	-2.57– -2.44
S.glacialis	-0.18	-0.2– -0.15	-16.59	-91.73– 58.56
S.boryi	-0.82	-0.85– -0.79	-1.60	-1.64– -1.56
T.serpylloides	-0.77	-0.80– -0.74	-2.49	-2.56– -2.43

Table S2 Likelihood ratio chi-square and model coefficients (standard error) for generalised linear models. The foundation species community and the subordinate species abundance are predictors of the species probability to survive or get secondary extinct. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Survival	**Secondary extinction**
Model estimation		
Community	$G_3^2 = 123.97 * **$	$G_3^2 = 3504.6 * **$
Abundance	$G_1^2 = 0.22$	$G_1^2 = 0.8$
Community x Abundance	$G_3^2 = 1.789$	$G_3^2 = 0.1$
Coefficients		
Open	-0.02 (0.27)	-0.16 (0.39) ***
Festuca	-0.76 (0.33) *	-1.63 (0.48) **
Arenaria	-0.81 (0.15) ***	-2.52 (0.21) ***
Plantago	-0.82 (0.103) ***	-1.77 (0.15) ***
Abundance	< 0.0001	< 0.001
Festuca x Abundance	< 0.001	< 0.001
Arenaria x Abundance	< 0.001	< 0.001
Plantago x Abundance	< 0.001	< 0.001

Plant species	
Arenaria tetraquetra	
Hormathophylla spinosa	
Sideritis glacialis	
Anthyllis vulneraria	
Jasione amethystina	
Lotus corniculatus	
Leucanthemopsis pectinata	
Leontodon boryi (Are)	
Crepis oporinoides (Hor)	
Chaenorrinum glareosum	

Pollinator species	
Apis mellifera	
Eristalis tenax	
Scythris iberica	
Xylocopa valga	
Bombus vestalis	
Lasioglossum cupromicans	
Megachilinae sp	
Bombus sp b	
Megachile parietina	
Bombus vestalis	
Megachile sp	
Scaeva albomaculata	
Bombus terrestris	
Hylaeus ibericus	
Bombus sp a	
Lampides boeticus	
Galeruca sp	
Panurgus cephalotes	

Figure S1 Plant species used in the experiment.

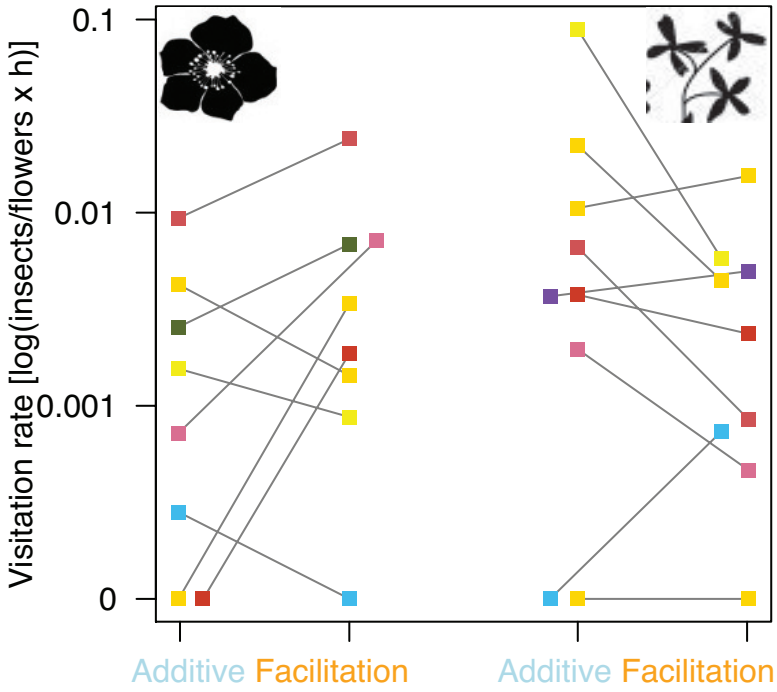

Figure S2 Pollinator visitation rate (calculated as the log of the ratio between pollinator abundance and flower abundance of each species per sampling hours) of each plant species, depicted with different colours, in *Arenaria* (left) and *Hormathophylla* (right) communities. Overlapping data points were slightly shifted horizontally for clarity.

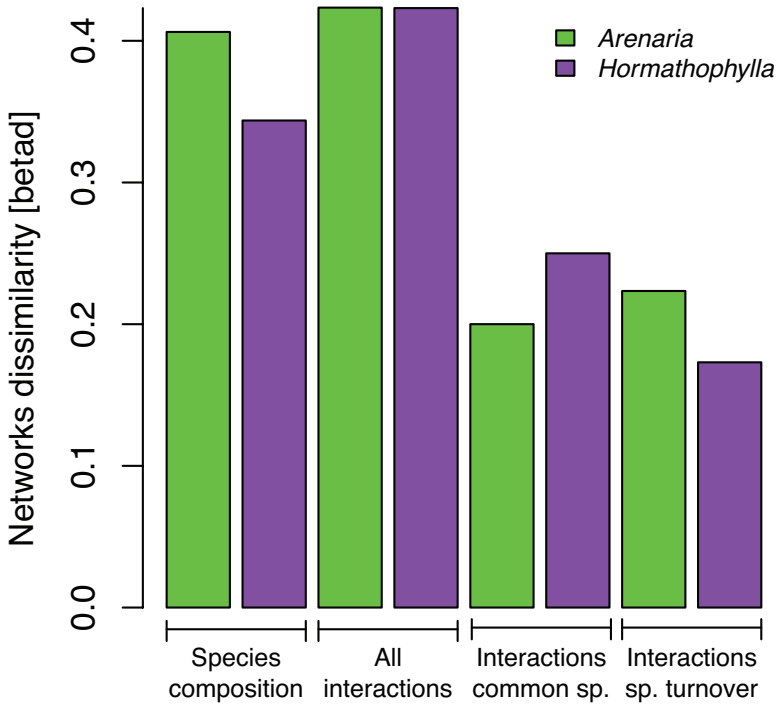

Figure S3 Dissimilarity components between sum and together networks of *Arenaria* (green) and *Hormathophylla* (blue).

Table S1 Summary of regression and mixed-effect models to analyse the change in pollinator diversity, pollinator visitation rate, relative nestedness, species interaction diversity and network robustness between the 'together' and 'sum' networks ('Network'), the foundation species *Arenaria* and *Hormathophylla* ('Foundation'), extinction scenario ('Scenario') and their interactions ('Scen:Net','Scen:Fs','Net:Fs','Scen:Net:Fs').

Response	**Predictor**	**Df**	**F**	***p***
Pollinator diversity	Network	1,52	0.97	0.3302
	Foundation	1,52	1.07	0.3061
	Net:Fs	1,52	11.00	0.0017
Visitation rate	Network	1,176	0.54	0.4640
	Foundation	1,176	1.46	0.2290
	Net:Fs	1,176	4.24	0.0409
Relative nestedness	Network	1,396	175.85	< 0.0001
	Foundation	1,396	3311.52	< 0.0001
	Net:Fs	1,396	21179.73	< 0.0001
Interaction diversity	Network	1,57	2.58	0.1137
	Foundation	1,57	1.75	0.1913
	Net:Fs	1,57	10.94	0.0016
Network robustness	Scenario	2,792	213.86	< 0.0001
	Network	1,396	37.41	< 0.0001
	Foundation	1,396	5.33	0.0215
	Scen:Net	2,792	195.07	< 0.0001
	Scen:Fs	2,792	12.28	< 0.0001
	Net:Fs	1:396	96.13	< 0.0001
	Scen:Net:Fs	2,792	33.67	< 0.0001

Table S2 Tukey HSD post-hoc tests performed on the regression models (i.e. Tab. SI1). Facilitation = 'fac', Additive = 'add', random scenario = 'Rnm', plant community = 'Pla', pollinator community = 'Pol'. Only comparisons of interest shown.

model	**Contrast**	q	**C.I. (95%)**	p
Pollinator diversity	Arenaria fac – Arenaria add	0.59	0.07–1.10	0.0187
	Hormathophylla fac – Hormathophylla add	-0.32	-0.83–0.19	0.3599
	Arenaria fac – Hormathophylla fac	0.60	0.08–1.11	0.0170
Visitation rate	Arenaria fac – Arenaria add	0.93	-0.40–2.26	0.2709
	Hormathophylla fac – Hormathophylla add	-0.57	-1.98–0.85	0.7259
	Arenaria fac – Hormathophylla add	1.21	-0.19–2.62	0.1177
Relative nestedness	Arenaria fac – Arenaria add	15.88	15.51–16.24	< 0.0001
	Hormathophylla fac – Hormathophylla add	-13.23	-13.59– -12.86	< 0.0001
	Arenaria fac – Hormathophylla add	20.31	19.94–20.67	< 0.0001
Interaction diversity	Arenaria fac – Arenaria add	0.48	0.12–0.84	0.0044
	Hormathophylla fac – Hormathophylla add	-0.17	-0.53–0.19	0.6144
	Arenaria fac – Hormathophylla add	0.45	0.09–0.81	0.0082
Network robustness	Rnm – Arenaria fac – Arenaria add	1.75	1.28–2.20	< 0.0001
	Rnm – Hormathophylla fac – Hormathophylla add	-0.23	-0.69–0.23	0.8984
	Rnm – Arenaria fac – Hormathophylla fac	0.79	0.33–1.26	< 0.0001
	Pol – Arenaria fac – Arenaria add	0.91	0.45–1.37	< 0.0001
	Pol – Hormathophylla fac – Hormathophylla add	-0.70	-1.16– -0.24	0.0001
	Pol – Arenaria fac – Hormathophylla fac	1.05	.059–1.51	< 0.0001
	Pla – Arenaria fac – Arenaria add	-2.02	-2.48– -1.55	< 0.0001
	Pla – Hormathophylla fac – Hormathophylla add	-1.83	-2.29– -1.36	< 0.0001
	Pla – Arenaria fac – Hormathophylla fac	-0.54	-1.01– -0.08	0.0069

Table S3 Contrasts among least-squares means of the regression models fitted for each extinction scenario (scenario (Scen): random (Rnm), plant community (Pla) and pollinator community (Pol)) with network robustness as response, interaction diversity as predictor (β) and its interactions with network type (network (Net): facilitation (fac) and additive (add)) and with foundation species (Fs: *Arenaria* (Are) and *Hormathophylla* (Hor)). Significance level for differences among groups: $\alpha = 0.05$. P-value adjusted with Tukey method. Degrees of freedoms= 395.

Scen	**Fs**	**Net**	β	ϵ	**group**
Rnm	Are	Add	0.24	0.42	1
Rnm	Are	Fac	0.81	0.46	2
Rnm	Hor	Add	0.62	0.45	3
Rnm	Hor	Fac	0.53	0.44	3
Pol	Are	Add	-0.32	0.42	1,2
Pol	Are	Fac	-0.17	0.46	1
Pol	Hor	Add	-0.17	0.45	1
Pol	Hor	Fac	-0.38	0.44	2
Pla	Are	Add	0.26	0.42	1
Pla	Are	Fac	0.39	0.46	1
Pla	Hor	Add	0.39	0.45	1
Pla	Hor	Fac	-0.16	0.44	2

Table S4 Empirical values and statistical significance of plant–pollinator networks for each foundation species (Fs; *Arenaria* (Are) and *Hormathophylla* (Hor)) and network type (Net; facilitation (Fac) and Additive (Add). For each network the table presents its number of plant species (Pl), pollinator species (Pol), number of interactions (L), connectance (C), the observed nestedness for the plant–pollinator networks (N), for the plants (N pl) and for the pollinators (N pol) with 95% confidence intervals.

Fs	**Net**	**Pl**	**Pol**	**L**	**C**	**N**	**N pl**	**N pol**
Are	Fac	7	27	47	0.249	0.357 (0.305–0.316)	0.278 (0.259–0.266)	0.436 (0.351–0.373)
Are	Add	6	24	31	0.215	0.350 (0.361–0.387)	0.217 (0.296–0.335)	0.482 (0.424–0.446)
Hor	Fac	8	18	24	0.167	0.195 (0.263–0.294)	0.113 (0.220–0.246)	0.278 (0.306–0.349)
Hor	Add	7	31	45	0.207	0.361 (0.319–0.336)	0.326 (0.268–0.289)	0.396 (0.370–0.383)

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Personal data

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Spoken languages:	Italian (native), English (fluent), Spanish (fluent)

Education

Ph.D. Ecology 10/2014–09/2017

University of Zurich & Life Sciences Zurich Graduate School Switzerland

Thesis: Plant interaction networks. Spatial dynamics, robustness and scaling up to pollinators

Advisors: C. Schöb, B. Schmid, J. Bascompte, R. Michalet (University of Bordeaux)

M.Sc. Natural Sciences *summa cum laude* 12/2011–04/2014

University of Milan Italy

Thesis: Plant–insect interactions in recently deglaciated areas

European mobility fellow 09/2010–07/2011

European Research Commission, University of Salamanca Spain

Major: Botany, biodiversity and climate change

B.Sc. Natural Sciences 10/2008–12/2011

University of Milan Italy

Thesis: Plant and insect assemblages in alpine debris-covered glaciers and rock glaciers

Publications

10. **Losapio G**, Schöb C & Pugnaire, F (*In prep.*) Age-based multilayer networks in a facilitation metacommunity.
9. Robinson, S.V.J., **Losapio G** & Henry, G.H.R. (*In prep.*) Flower-power: flower diversity is a stronger predictor of network structure than insect diversity in an Arctic plant–pollinator network.
8. **Losapio G**, Fortuna MA, Bascompte J, Schmid B, Michalet R, Neumeyer R, Baur H, Castro L, Cerretti P, Germann C, Haenni J-P, Klopfstein S, Müller A, Ortiz J, Pont AC, Rousse P, Schmid J, Schwarz M, Sommaggio D & Schöb C (2017) Facilitation between plants shape pollination networks. *bioRxiv*, 161034. https://doi.org/10.1101/161034
7. **Losapio G**, De la Cruz M, Escudero A, Schmid B & Schöb C (2017) Positive interactions support complex networks. *bioRxiv*, 118166. https://doi.org/10.1101/118166

6. Tian D, Jian L, Ma S, Fang W, Schmid B, Xu L, Zhu J, Li P, **Losapio G**, Jing X, Zheng C, Shen H, Zhu B, & Fang J. (*in press*) Effects of nitrogen deposition on soil microbial communities in temperate and subtropical forests in China. *Science of the Total Environment*.
5. **Losapio G** & Schöb C (2017) Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. *Functional Ecology*, 31, 1145-1152. `https://doi.org/10.1111/1365-2435.12839`
4. Gobbi M, Ballarin F, Brambilla M, Compostella C, Isaia M, **Losapio G**, Maffioletti C, Seppi R, Tampucci D, & Caccianiga M. (*in press*) Life in harsh environments: carabid and spider trait types and functional diversity on a debris-covered glacier and along its foreland. *Ecological Entomology*.
3. **Losapio G** (2016) Plant interaction networks' response to environmental changes. *Plant Science Center Newsletter*, 29, 6.
2. **Losapio G**, Gobbi M, Marano G, Avesani D, Boracchi P, Compostella C, Pavesi M, Schöb C, Seppi R, Sommaggio D, Zanetti A & Caccianiga M (2016) Feedback effects between plant and insect communities along a primary succession gradient. *Arthropod–Plant Interactions*, 10, 485-495. `https://doi.org/10.1007%2Fs11829-016-9444-x`
1. **Losapio G**, Jordán F, Caccianiga M & Gobbi M (2015) Structure-dynamic relationship of plant–insect networks along a primary succession gradient on a glacier foreland. *Ecological Modelling*, 314, 73-79. `https://doi.org/10.1016/j.ecolmodel.2015.07.014`

Grants and awards

Travel grant, University of Zurich (1000 CHF)	2015–2016
SNSF Ambizione, awarded to C. Schöb (600000 CHF)	2014–2017
Poster award, International Plant Science Conference	2014
Biodiversity monitoring project, Stelvio National Park (3500 EUR)	2014
Flora award, Naturalistic and Scientific Photography UniMi	2012
European mobility fellowship Erasmus, European Research Commission (3000 EUR)	2010–2011
University scholarship, Italian Social Service (2500 EUR)	2009–2014

Teaching

Organized & taught

Community Ecology 06/2016
Ph.D. students, Life Science Zurich Graduate School

Plant Systematics and Identification 05/2015
Ph.D. students, Life Science Zurich Graduate School

Mentoring

Elizabeth Norton, *M.Sc. Environmental Sciences*, University of Zurich 2016–2017

Tutoring, *University, high and secondary school students*, Como 2008–2014

Assistance

Publishing in science 08/2016
M.Sc. and Ph.D. students, Peking University

Ecology and Biodiversity 2015–2016
B.Sc. Biology, University of Zurich

Introduction to Statistics 03–05/2015
B.Sc. Environmental Sciences, University of Zurich

General and Systematic Botany 02–06/2014
B.Sc. Natural Sciences, University of Milan

Invited lectures

Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes 04/2017
Biodiversity, Macroecology and Evolution, WSL, Switzerland.

Multivariate analysis of vegetation and ecological data: the example of PCA and CCA 05/2014
Data sampling and statistical analysis, M.Sc. Natural Sciences, University of Milan

Geophysics and ecological features of rock glaciers 01/2012
Climatic Geomorphology, M.Sc. Natural Sciences, University of Milan

Outreach 05/2017

Promotion and conservation of urban forests. *Public debate and campaign*, Como

Leaving for Erasmus. *Promotion of EU universities student exchange*, University of Milan 11/2015

Scientifica, *Public science communication*, ETH & University of Zurich 09/2015

Natural Sciences Info Days, *High school students*, University of Milan 06/2014

Flora and fauna of our mountains, *Primary school students & CA*I, Como 05/2014

Research activities

Visiting scholar 05/2016
Group of Biodiversity and Conservation, University King Juan Carlos

Researcher as PhD student 10/2014–09/2017
Teaching, experiments, data analysis and communication, University of Zurich

Botanist 06/2014–09/2014
Biodiversity of alpine ecosystems, Stelvio National Park

Research assistant 06/2013–06/2014
Plant functional trait database, Department of Biosciences, University of Milan

Internship 10/2012–01/2013
Interreg IVC, Laboratory of Archeobiology, Museum of Como

Reviewer

Arthropod–Plant Interactions; Ecological Complexity; Ecology and Evolution; Journal of Arid Environments; Journal of Forestry Research; Journal of Plant Ecology; Journal of Theoretical Biology; Journal of Vegetation Science; Oikos.

Conferences & presentations

Invited talks

Losapio G & Schöb C, Network response to environmental changes: integrating plant interaction, network theory and functional traits. Ecological Society of America annual meeting, August 6–11 2017, Portland, USA.

Losapio G Complex synergies among plants shape pollination network functioning. Behaviour, Ecology, Environment and Evolution Seminar, May 30 2017, University of Zurich, Switzerland.

Contributed talks

Losapio G, Unifying interaction patterns and processes: a network perspective on plant communities. Workshop: Biotic Interactions, March 27–31 2017, Life Science Zurich Graduate School, Switzerland.

Losapio G, Network response to environmental changes: integrating plant interaction, network theory and functional traits. Ecology Mini-Symposium, March 1 2017, Life Science Zurich Graduate School, Switzerland.

Losapio G, Schmid B & Schöb C, Scaling up interactions: plant associations drive pollination network functioning. Medecos-AEET meeting, February 1–4 2017, University of Sevilla, Spain.

Losapio G, De la Cruz M, Escudero A, Schmid B & Scöb C, The spatial dimension of plant association networks. British Ecological Society annual meeting, December 11–14 2016, Liverpool, UK.

Losapio G & Schöb C, Plant interaction networks' response to environmental changes. Biology 16, the Annual Swiss Conference on Ecology, Evolution, Systematics, Biogeography and Conservation, February 11–12 2016, University of Lausanne, Switzerland.

Losapio G & Schöb C Facilitative interactions increase stability of plant–plant networks under different environmental change scenarios. Ecological Networks Symposium, September 7–8 2015, University of Bristol, UK.

Losapio G Plant–insect networks along a primary succession gradient. Rigi Workshop on Mathematical and Computational Modelling in Life Sciences, Swiss Academy of Sciences, January 18–20, 2015, Switzerland.

Losapio G, Jordán F, Caccianiga M & Gobbi M, Plant–anthophilous insect ecological networks along a glacier foreland chronosequence. Eighth European Conference on Ecological Modelling, October 27–30 2014, Université Cadi Ayyad, Morocco.

Tampucci D, Caccianiga M, Gobbi M, **Losapio G**, Maffioletti C, Flora and fauna of rock glaciers and debris-covered glaciers. Scientific meeting of the Italian Botanical Society, March 1 2013, Museum of Natural History of Milan, Italy.

Contributed poster

Losapio G & Schöb C, Facilitative interactions increase stability of plant–plant networks under different environmental change scenarios. Plant Science Center Symposium, December 3 2015, ETH, Switzerland.

Losapio G, Gobbi M, Marano G, Compostella C, Boracchi P & Caccianiga M.Relationship between plant and flower-visiting insects along a debris-covered glacier foreland. Workshop: Ecology of glacier forelands, September 17–21 2014, University of Innsbruck, Austria.

Losapio G, Gobbi M, Marano G, Compostella C, Boracchi P & Caccianiga M (*Awarded*), Linking plant reproductive success and flower-visiting insects along a debris-covered glacier foreland. International Plant Science Conference, Italian Botanical Society, September 2–5 2014, Italy.

Research workshops

Biotic Interactions. Mechanisms and Functions, *Life Sciences Zurich Graduate School*	03/2017
Early Careers Workshop, *British Ecological Society*, UK	12/2016
Mathematical and Computational modelling in Life Sciences, *Swiss Academy of Sciences*	01/2015
Advanced Course in Ecological Modelling, *ISEM*, Morocco	10/2014
Summer School in Alpine Field Ecology, *University of Innsbruck*	08/2013

Continuing education

Introduction to Functional Genomics, *Plant Science Center*	07/2017
Writing a Post-Doctoral Grant, *Plant Science Center*	11/2016
Recent advances in Biocommunication, *ETH*	FS/2016
Project management for research, *Graduate campus UZH*	04/2016
Scientific Writing, *Graduate campus UZH*	12/2015
Mixed Models, *Life Sciences Zurich Graduate School*	05/2015
Complex Networks, *ETH*	SS/2015
Macroecology, niche evolution and climate change, *WSL & UZH*	12/2014
Generalized Regression, *University of Zurich*	FS/2014
Ecology and Evolution, *Life Sciences Zurich Graduate School*	FS/2014
Plant Ecology Journal Club, *Life Sciences Zurich Graduate School*	FS/2014

Professional society membership

Ecological Society of America (since 2017)

British Ecological Society (since 2016)

Italian Ecological Society (2015)

Board commitee

Life Science Zurich Graduate School, PhD Program in Ecology	2015

Skills

Project management
Public communication
Work independently and collaborate in team
Computational modelling
R programming
Network theory
Data analytics
Fieldwork, experimental design and sampling methods
Passionate of flora and natural history
Italian Alpine Club diplomas in mountaneering
Editing in LaTeX
Erdős number: 5